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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

155th Session (1942–43) Part 2

CONTENTS

Page

Proceedings, 11 February 1943 69

The chromatographic separation of plant pigments and some remarks upon the significance of the absence of chlorophyll B from certain Classes of Algae. By A. C. Gardiner. [Title only.] 70

An Amphipod, Orchestia bottae, new to Britain. By Isabella Gordon 70

A new Catfish with a remarkable swim-bladder. By Ethelwynn Trewavas 70

Proceedings, 25 February 1943 72

Experimental studies of the selective actions of Predators. By E. J. Popham. [Title only.] 72

Variation in the flowers of Fuchsia hybrida hort. By B. Barnes 73

Geographical distribution of the genus Paeonia. By F. C. Stern 76

[*For continuation of Contents see back page.*]

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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

155th Session (1942–3) Part 2

PROCEEDINGS OF THE GENERAL MEETING
11 February 1943

held jointly with The Zoological Society of London

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 26 November 1942, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Prof. G. D. Hale Carpenter, Mr. A. H. Hamm, Mr. Ko Zen Kuang, Mr. W. S. Lacey, Mr. C. McCann, Mr. C. R. Orton, Dr. C. E. Raven, Dr. E. S. Russell, Prof. F. E. Weiss and Dr. J. C. Willis.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted,—Mr. George Woodrouffe Harris, Prof. Alexander James Edward Cave, Mr. James Maxwell McConnell Fisher and Dr. Charles Aubrey Hamilton Franklyn.

Read for the first time certificates of recommendation of the following candidates for Fellowship,—in favour of Dr. Raphael Ernest Grail Armattoe, M.Litt., Capt. James Percy Tufnell Burchell, M.C., Emlyn Glyndwr Davies, Michael Curtis Rawlence and Dr. John Smart.

The President reported the death of The Most Hon. The Marquess of Headfort, F.L.S.

The President reminded Fellows that they are invited to make recommendations for new Members of Council and Officers.

The following communications were read and discussed :—

Dr. Isabella Gordon. Exhibition of an Amphipod (*Orchestia bottae* M.-Edw.) new to the British Fauna. (Discussed by Dr. R. Melville, Dr. Malcolm Smith and the President.) [Printed in full, p. 70.]

Dr. Ethelwynn Trewavas. A new species of Catfish with a remarkable swim-bladder. (Communicated by the Zoological Secretary. Discussed by Dr. F. R. Irvine, Mr. R. H. Burne, Dr. C. C. Hentschel and Dr. L. R. Wheeler ; Dr. Trewavas replied.) [Printed in full, p. 70.]

Mr. A. C. Gardiner. The chromatographic separation of plant pigments and some remarks upon the significance of the absence of chlorophyll B from certain Classes of Algae. (Discussed by Prof. T. M. Harris; Mr. A. C. Gardiner replied.)

AN AMPHIPOD, ORCHESTIA BOTTAE, NEW TO BRITAIN.

By Dr. Isabella Gordon.

In September 1942 Dr. F. van Emden told me that his son had seen many Amphipods hopping about, above high-water mark, on the banks of the river Thames about 100 yards beyond Isleworth Ferry, Richmond. He thought they must belong to the genus *Orchestia*, but had never seen the genus so far from the sea. I asked him to collect some specimens for me and, on examining them, they seemed to agree with the description and figures of *Orchestia bottae* M.-Edw. given by Fage in 'Faune de France' (IX, Amphipoda, p. 276, fig. 286; 1925). The Amphipods were present in large numbers under stones a short distance below the towpath, and were dark brown in colour. As soon as the stones were overturned they hopped about so quickly, seeking a new hiding-place, that it was by no means easy to catch them.

Orchestia bottae is the most terrestrial species of the genus and has been recorded from the Black Sea area, Palestine, Cyprus (at an altitude of 1255 m.), N. Italy (near Trieste, Venice and all round the shores of Lake Garda), France (in various localities far from the sea, e.g. Cambrai, Nancy, usually near streams and canals, and from a well at Nantes), Holland (in a garden 80 kilometres from the sea), Belgium, Germany (by the Flakensee, Berlin) and East and South Africa.

It has long been known that various terrestrial species of the family Talitridae have been transported long distances in the soil round the roots of plants, and have succeeded in establishing themselves in gardens or in the conservatories of Botanical Gardens. *Orchestia bottae* may have been introduced into Kew Gardens along with plants from the Continent. On the other hand, as the Thames embankment was being built up just beyond the spot where the specimens were found, they may have come in the sand that was brought in barges to the place where repairs were in progress.

A NEW CATFISH WITH A REMARKABLE SWIM-BLADDER.

By Dr. Ethelwynn Trewavas.

Among the Gold Coast fishes sent to the British Museum (Natural History) from time to time by Dr. F. R. Irvine are three specimens of a Schilbeid fish which, although having the external appearance of a *Eutropius*, is found upon dissection to possess a long posterior appendage to the swim-bladder, extending back in the tail, on the right side of the haemal spines, to near the posterior end of the anal fin. This peculiarity is known to Gold Coast fishermen, who demonstrated to Dr. Irvine the difference between this and a species of *Eutropius* caught with it in the river Volta.

The species of *Eutropius* are silvery catfishes with compressed body and depressed head, with a short rayed dorsal fin and a small adipose, and with a long anal fin of 45 to 70 rays. The air-bladder is of a generalized Siluroid type, externally undivided, but internally incompletely divided into an anterior chamber and a posterior. Laterally the bladder extends outwards between the muscles to meet the skin in an oval area. The fibres of the wall of the anterior chamber are, as in other Siluroidea, intimately connected with the *tripus*, one of a short chain of ossicles which connect the air-bladder with a fenestra in the skull, and so, through the perilymph cavity, transmit vibrations from the air-bladder to the internal ear, thus being analogous to the mammalian auditory ossicles. In some species of *Eutropius* this typical bladder extends above the peritoneum for about three-quarters of the length of the abdomen ; in others it is much shorter, confined to the anterior quarter of the abdominal region.

The typical part of the bladder of the new fish resembles the shorter type and is separated by a narrow constriction, barely perforated, from the posterior caecum. This caecum is again constricted at intervals, and its walls are thickened and ridged by fibrous tissue. Its function is obscure.

Other catfish in which the air-bladder has a posterior caecum are *Pangasius pangasius* and *Cryptopterus* spp., Indian and Malayan members of the related families of Pangasiidae and Siluridae respectively. In *Pangasius*, which has the anal fin well developed, but much shorter than in the Schilbeidae, the development of the caecum has been traced by Nair (1937) from a mere papilla in a specimen of 91 mm. total length to about 375 mm. in a specimen of 885 mm. In *Cryptopterus*, which has a very long anal fin and no dorsal, there is no constriction between the caecum and the normal part of the bladder.

The systematic position of the new species is still undecided.

Discussion.—

Dr. F. R. Irvine.—The catfish described by Dr. Trewavas was collected during a small Volta River expedition financed by Achimota College, Gold Coast, in April 1938. The expedition found that shoals of Schilbeid catfishes were being caught in spiral cast-nets from canoes at Atimpoku, above the Senchi Rapids. Among them was a *Eutropius* which appeared slightly different from *E. niloticus* and had a different vernacular name. There was also a closely similar species, for which the fishermen had a distinct name, which they justified by slitting the body backwards from the anus to the tail end, displaying the curious structure which was reported to the British Museum and subsequently studied and now described by Dr. Trewavas. This fish had been feeding on small Crustacea ; the *Eutropius* had fish-remains in the stomach.

Mr. R. H. Burne asked what the relation was of the peritoneum to this curious structure.

Dr. C. C. Hentschel asked if Dr. Trewavas had noticed any structural difference between the portions of the swim-bladder in the abdominal and caudal regions which might give some indication of the functions of the two parts.

Dr. L. Richmond Wheeler enquired if anything was known about the development of this remarkable 'caecum' of the swim-bladder, adding it would be interesting to know if it forced its way, apparently with a corresponding extension of the coelom, from the anterior region backwards among the muscles of the long post-anal tail.

Dr. Trewavas, in reply, stated that both the main part of the swim-bladder and its caecum are, as usual, outside the peritoneum, which does not extend back into the tail with the caecum.

The dissection of the new fish is incomplete, but so far special peritoneal sacs for the liver have not been detected.

PROCEEDINGS OF THE GENERAL MEETING
25 February 1943

held jointly with The Zoological Society of London

Dr. E. S. Russell, O.B.E., M.A., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 11 February 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Prof. J. McLean Thompson, Prof. F. E. Weiss and Dr. J. F. G. Wheeler. The Botanical Secretary called attention to Prof. McLean Thompson's donation—a MS. copy of his paper, 'A study in modern Angiospermy, with special reference to the Carob tree (*Ceratonia Siliqua* L.)'.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted,—Frank David Armitage.

Read for the second time certificates of recommendation of the following candidates for Fellowship,—in favour of Dr. Raphael Ernest Grail Armattoe, M.Litt., Capt. James Percy Tufnell Burchell, M.C., Emlyn Glyndwr Davies, Michael Curtis Rawlence and Dr. John Smart.

Proposed Alterations in the Bye-Laws were read from the Chair for the first time, and copies in print were distributed.

The following communications were read and discussed :—

Dr. B. Barnes. Abnormal flowers of the garden *Fuchsia*. Discussed by Mr. W. C. Wordsell ; Dr. Barnes replied.) [Printed in full, p. 73.]

Colonel F. C. Stern, O.B.E., M.C. The geographical distribution of the genus *Paeonia*. (Read by the Botanical Secretary, in Colonel Stern's absence. Discussed by Prof. F. E. Weiss, Dr. J. Ramsbottom and Madame Skalińska.) [Printed in full, p. 76.]

Dr. E J. Popham, Ph.D., F.Z.S. Experimental studies of the selective actions of Predators. (Communicated by the Zoological Society. Discussed by Dr. Malcolm Smith, the President, Mr. I. H. Burkill, Dr. R. Melville ; Dr. Popham replied.)

This paper will be published in the 'Proceedings of the Zoological Society'.

VARIATION IN THE FLOWERS OF FUCHSIA HYBRIDA HORT.

By B. Barnes.

In the summer of 1939 two plants of *Fuchsia hybrida*, variety 'Tower of London', bore, scattered haphazard among hundreds of normal tetramerous flowers, ten symmetrically trimerous flowers and three others having some special peculiarity. The trimerous flowers need little comment. They differed from normal only in being trimerous. Such flowers have been seen a number of times on plants of 'Tower of London' in the Royal Botanic Gardens, Kew, and, maybe, a tendency towards trimery is a character of the variety.

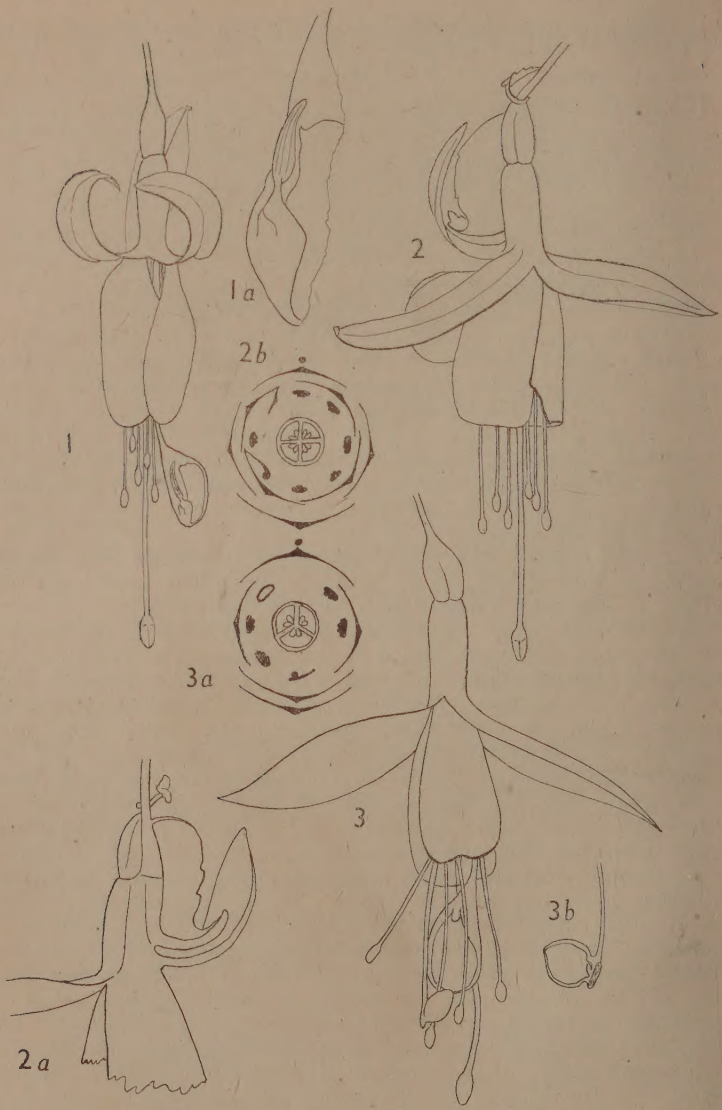
The three more exceptional flowers require separate description.

Flower A (figs. 1, 1*a*).—Flower A opened on 20 June 1939 and fell on 3 July. It was trimerous in all its whorls, and ordinary in size and colour. One of the three antepetalous stamens was replaced by a large pendulous funnel, coloured like the petals except in its long whitish stalk. A small, dull yellow lump (the normal anthers were dull purple) was turned back against the outer surface of the funnel, and, except at its tip, was fused with that surface. A section showed that this appendage contained a number of loose, collapsed, thin-walled cells, but no recognizable pollen grains.

The regular trimery of the flower and the position of the funnel suggest that it was a monstrous stamen, with one lobe of the anther imperfect and fertile, the other changed into a petaloid expansion.

Flower B (figs. 2, 2*a*, 2*b*).—Flower B was first noted on 14 June 1939 as a well-formed bud, distinguished by the presence of a leafy outgrowth attached to the side of the ovary and of the calyx tube, and by a small leaf, with a tiny reddish outgrowth opposite to it, springing from the flower-stalk just before that joined the ovary. The flower opened three days later. It was detached for examination on 13 July, by which time the three next youngest flowers on the branch had opened and had fallen. They were ordinary tetramerous flowers. Flower B thus remained open on the plant for some twenty-five days, whereas the normal flowers lasted for from a week to ten days. At the time of picking, the flower-stalk was still firmly attached to the branch; ordinarily, old flowers of *Fuchsia* fall very readily. When the flower was handled, instead of the calyx tube separating from the ovary, as is usual in old flowers, it remained firmly attached, and, contrary to the general condition, the flower-stalk came away from the base of the ovary. That stalk, with its attached leaf, was planted on damp, sterilized soil in the hope that it would root, but *Botrytis cinerea* put an end to the experiment.

The calyx was trimerous, with sepals normal in colour and size, but not in arrangement, for they were so set that the midribs of two were almost in a straight line, the third sepal lying midway between them in the exterior angle. There was thus a wide gap on one side of the flower. Here there was a normal petal, with a second normal petal following, then a third petal with one edge bent inwards about a shallow sinus; a fourth, distinctly and unevenly bilobed by a deep sinus extending some two-thirds of the way into the petal, completed the corolla. One



Fuchsia hybrida hort. Abnormal flowers.

Flower A.—General appearance (1) and enlarged view of aborted anther lobe (1 *a*).
Flower B.—General appearance (2), with the projecting petal at the back; attachment of leaf to ovary and calyx tube (2 *a*); floral diagram (2 *b*).
Flower C.—General appearance (3); floral diagram (3 *a*); enlarged view of the stamen, with one fertile anther lobe and an ear-shaped expansion (3 *b*).

The whole flowers are drawn to half natural size. The dimensions of the other drawings may be estimated from those of the flowers.

lobe of the petal stood out from the flower, giving a very untidy appearance. The six stamens and the four-carpellary gynaeceum seemed to be normal.

The small leaf on the flower-stalk differed from the foliage leaves only in being about one-eighth normal size. One-half of the leafy expansion attached to the side of the ovary and calyx tube was equivalent in size and characters to one-half of an average leaf. On the other side of the tip of the distinct midrib there was a small amount of normal leaf tissue, but most of that side was red, thick and fleshy, firmly attached to the ovary, and loosely united with the calyx tube. This outgrowth may have been the partner of the small leaf, carried up on to the ovary wall and calyx tube, but the presence of a probable leaf rudiment on the flower-stalk, opposite to a leaf, as well as the position of these parts, are against that interpretation.

The malformed petals bore nothing which looked like an anther, though one had a small yellow fleck at its tip; that fleck was not swollen and contained nothing unusual. The flower was tetramerous in the gynaeceum, and fundamentally so in the corolla. It seems very likely that the two-lobed petals were really composite in nature, chiefly petals, but with a hint of a stamen attached to each.

In this flower the physiological balance seems to have been shifted towards the vegetative side, with a notable lengthening of the life of the flower. That may have been favoured by an increased local supply of nutriment from the associated leaves, but the production of these leaves and the long duration of the flower may together have been due to some more deep-seated change.

Flower C (figs. 3, 3*a*, 3*b*).—Flower C developed in early September 1939: it was of ordinary colour and length. There were two sepals and two petals, all normal, four normal stamens, two additional structures almost certainly malformed stamens, and a tricarpellary ovary. The flower was, therefore, dimerous in the perianth, trimerous in the androecium and gynaeceum; the instability in the androecium may be associated with the change-over in the meristic relations.

Of the modified stamens, one had one anther lobe containing apparently good pollen, the other lobe being changed into a small ear-like expansion coloured like a petal. The second was a small funnel, in general like that already described in Flower A. It was coloured like a petal, except for a small yellow tongue in the notch of the opening. That tongue did not contain pollen.

Comments.

There seems no doubt that the florists' *Fuchsia*, while perhaps based on *F. fulgens*, is a complicated hybrid to which several species from Central and South America have contributed, and for that reason the plant is here called *F. hybrida* hort. It is not remarkable that a plant of such mixed parentage should be capricious in behaviour, but even so, the abnormalities which have been described invite comparison with the normal conditions in some other members of the Onagraceae. Dimery, presumably by suppression, is familiar in the Enchanter's nightshade (*Circaea*), and the funnels are somewhat reminiscent of the anterior staminode of *Lopezia*. *Lopezia*, indeed, suggests a problem. It might well be that a detailed study of the development of the flower of that

plant would show that the strange upper petals there are not really petals, but, possibly, composite structures in which petals and stamens are combined.

Discussion.—

Mr. W. C. Worsdell.—Certain abnormalities of the calyx, observed by Masters, myself and others, and apparently shown in part by one of the author's figures, suggest that the perianth in *Fuchsia* is, in reality, inserted *below* the ovary, the false appearance of 'inferior ovary' being due to intimate adnation of basal part of perianth to ovary wall. Morphologically, the 'inferior ovary' has no existence in actual fact. Abnormal cases of *Oenantha* (Umbelliferae) and *Pirus* (Rosaceae), in which calyx is clearly inserted at *base* of ovary, support this view.

Trimerous flowers in *Fuchsia* are quite frequent. Zygomorphic flowers have also been described.

As regards *doubling* of flower, Goebel figures buds in which multiplication of petals takes place by both collateral and serial (radial) division of the petal rudiments.

GEOGRAPHICAL DISTRIBUTION OF THE GENUS PAEONIA.

By F. C. Stern, O.B.E., M.C., F.L.S.

H. N. Barber referred in a short article in 'Nature' (vol. cxlviii, p. 227; 23 August 1941) to the evolution of the genus *Paeonia* and the investigations and details of the geographical distribution which was to be found in the forthcoming study of the genus written by me. Owing to the war conditions this study will not be published by the Royal Horticultural Society till after the War. The cytological aspect of the genus and its relation to the geographical distribution has been referred to at meetings of the Linnean Society, so a short paper on the subject may be of interest to the Fellows.

The John Innes Horticultural Institution has been kind enough to study the different species of Paeonies from the cytological point of view and to inform me of the chromosome numbers in plants that I supplied to the Institution of each species under the names used in the study, as it is difficult to be sure that a plant referred to by different writers under a certain name is always that plant. This is especially the case with Paeony species.

The basic chromosome number throughout the genus is 5; size and morphology of the chromosomes differ little in the Old World species; but the American species are distinguished cytologically from the Old World species by the terminal localization of pachytene pairing and extensive reciprocal interchange of chromosome segments. Some Paeony species have 20 as their somatic chromosome number instead of 10, that is, some species are tetraploids ($2n=20$) and some are diploids ($2n=10$). It has not been possible to obtain the chromosome numbers of all the species, but sufficient are now known to made this study suggestive.

The distribution of the genus is confined to the northern hemisphere. Two species only are found in North America on the west coast, the remainder are distributed across Europe and Asia, from Spain to Japan

with 25 species and varieties or subspecies in Europe, including Morocco and Algiers and Asia Minor, and 19 species and varieties or subspecies in Asia. The shrubby species are only found in Asia, and all the shrubby species are diploids.

The species separate themselves into groups allied together by their morphological characters. The species grouped together in this way were found to be located in the same geographical area, in some cases large areas and in others small. In several of the groups there are no tetraploid species, and in two cases there are no diploid species, but in the majority of groups it will be found that one species is diploid and the remainder of the species are tetraploids. The table below gives the groups showing the diploid and tetraploid species.

Species in Paeonia.

	Group.	Diploid.	Tetraploid.
N. America.	—	Two diploid species.	No tetraploids.
Europe.	1	*P. tenuifolia* (Transylvania to Caucasus).	No tetraploid.
	2	No diploid.	*P. peregrina* (Balkans).
	3	*P. Clusii* (Crete).	*P. officinalis* (N. Italy). *P. humilis* and variety (S. France and Spain).
	4	*P. Broteri* (Portugal).	No tetraploid.
	5	No diploid.	*P. coriacea* (S. Spain and N. Africa).
	6	*P. rhodia* (Rhodes).	*P. arietina* (Asia Minor). *P. Bakeri* (cultivated).
	7	*P. daurica* (Crimea).	*P. mascula* (Central Europe). *P. banatica* (Hungary).
	8	*P. Cambessedesii* (Balearics).	*P. Russi* and two varieties (Corsica, Sardinia and Sicily).
	9	*P. Mlokosewitschi* (Caucasus).	*P. Wittmanniana* and two varieties (Caucasus).
Asia.	10	*P. japonica* (Japan).	*P. obovata* and variety (E. Asia).
	11	*P. Veitchii* (W. China).	No tetraploids.
	12	*P. anomala* (NE. Russia and Central Asia).	No tetraploids.
	12	*P. lactiflora* (NE. Asia). *P. emodi* (N. India).	No tetraploids.
	13	*P. Delavayi* (W. China). *P. lutea* (W. China). *P. Potanini* (W. China).	No tetraploids.
	14	*P. suffruticosa* (W. China).	No tetraploids.

The above table shows how the different species grouped together by their morphological characters have, where there are tetraploids and diploids in the same group, one diploid species and one or more tetraploid species in each group. In each group the diploid and allied tetraploid species are in the same geographical area. They do not always occupy the same territory, and, where there are both diploid and tetraploid species, the diploids have the more restricted range.

The diploids, *P. Clusii*, *P. rhodia*, *P. Cambessedesii* and *P. japonica*, are confined to islands. *P. daurica* to the Crimea and nearby districts, and *P. Mlokosewitschi* to one small district in the central Caucasus. The tetraploid species, on the other hand, have a wider range. The same phenomenon is discussed by Anderson and Sax in reviewing the *Tradescantia* species allied to *T. virginiana* in North America ; they show that the diploid species have in each case a comparatively narrow range and the tetraploids have a very wide distribution. Again, Manton, in discussing 'the problem of *Biscutella laevigata*' and the distribution of the species in Central Europe, says that the diploid and tetraploid forms do not occupy the same territory, and in few places do the localities even abut ; the tetraploid forms have spread into an area which was covered largely by the Alpine Ice Sheet, while the diploid forms are practically confined to unglaciated regions ; it is suggested that the diploid forms are inter-glacial, if not pre-glacial relics, survivors of the pre-glacial period ; the tetraploid forms occur in nearly the whole area occupied by the Alpine Ice Sheet during the Glacial Period, therefore these tetraploids must be post-glacial immigrants to many of their present districts and may still be spreading. The diploid forms give little evidence of expansion of territory and show highly disrupted 'Areal' centring round river systems known to be favourable climatically and to be rich in 'relics' of various kinds.

This explanation may be applicable to the distribution of Paeony species to explain the reasons why the tetraploid species in Europe are so much more numerous than the diploid species, and why in Asia and America the diploid species so greatly outnumber the tetraploids.

The suggestion is that in Europe, in the Glacial Period, the diploid species which are presupposed to be pre-glacial relics were pushed down on to the islands and into other warm outlying districts south of the glacial area. The tetraploid species, which are presupposed to have arisen from the diploid ones, proved themselves better adapted to the post-glacial conditions and have spread more rapidly than the diploids, owing to their more vigorous habits. The European tetraploid species in cultivation are stronger growing plants and increase faster than the European diploid species. The tetraploid species have been responsible for the post-glacial migrations northward and, where possible, southward ; it was only possible for them to spread south to the mountains of Morocco and Algeria, owing to the Mediterranean and the desert conditions of the rest of North Africa. This hypothesis would explain how groups of Paeonies which are closely allied morphologically are found in the same geographical areas in Europe with one diploid species confined to a limited area and one or more tetraploid species with a much larger distribution. For instance, the diploid *P. Clusii* is restricted to the island of Crete, while the other species of the *officinalis* group cover the maritime districts of Albania and Trieste, through northern Italy, southern France and central Spain ; again, the diploid *P. rhodia* is restricted to the island of Rhodes, while the allied tetraploid *P. arietina* covers all Asia Minor ; again, the diploid *P. daurica* is found in the Crimea and nearby districts, while *P. mascula* is found throughout central Europe ; again, the diploid *P. Cambessedesii* is only found in the Balearic

Islands and the other species and varieties of the *Russi* group, all tetraploids, cover the larger areas of the islands of Corsica, Sardinia and Sicily; again, the diploid *P. Mlokosewitschi* is restricted to one small district in the central Caucasus, and the other species and varieties of the *Wittmanniana* group cover the whole of the Caucasus range, even stretching down to the mountains of northern Persia. The same phenomenon occurs in eastern Asia with the *obovata* group; the diploid *P. japonica* is only found in Japan, but *P. obovata* and its variety, both tetraploids, are found over a wide area on the mainland of eastern Asia.

The remainder of the Paeony species in Asia and western North America are diploids, some covering large areas and some small. It is supposed that these species have not been displaced during the Glacial Period, but survived in areas not covered by the glacial sheet. The diploid species from the mainland in Asia are strong growing plants in cultivation and increase rapidly.

In Europe there are two diploid species—*P. Broteri* and *P. tenuifolia*—which have no allied tetraploid species; there are also two tetraploid species—*P. peregrina* and *P. coriacea*—which have no allied diploid species. From the two diploid species it would appear that no tetraploid forms have arisen, while the tetraploid species may have arisen from diploid species which have died out.

It is difficult to draw definite conclusions from the facts, but it may be permissible to speculate on a possible explanation, and this hypothesis is put forward as a speculative suggestion to explain the main features of the geographical distribution of the genus.

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Anderson, E., & Sax, K. 1936. Cytological Manual of the American species of *Tradescantia*. *Bot. Gaz.*, xcvii, no. 3.

Manton, L. 1934. Problem of *Biscutella laevigata*. *Zeitschr. für Induktive Abstammung*, lxvii.

Discussion.—

Dr. Maria Skalińska. As pointed out by Colonel Stern, the areas of diploid species are in most cases smaller than those occupied by the corresponding polyploids, for the doubling of the number of chromosomes which occasionally occurs in nature (through mutation or in consequence of hybridization) causes morphological and physiological changes which enable the newly formed types to advance into localities which were inaccessible to their diploid ancestors. In his studies on desert plants Hagerup ('Ueber Polyploidie in Beziehung zu Klima, Oekologie und Phylogenie. Chromosomenzahlen aus Timbuktu', Hereditas, xvi, pp. 19–40: 1932) found that the polyploid types are more vigorous and more resistant than the related diploids, and they are able to develop in the highly unfavourable desert climate, whereas the diploids are restricted to small areas.

It should be added, however, that sometimes it is the diploid species which has a wider distribution than the presumably younger polyploid form, e.g. the range of the diploid species *Anemone silvestris* ($n = 8$) is wide in Europe and Asia, but the closely related tetraploid species

A. rupicola ($n=16$) occupies a small area confined to the Himalaya Mts., where it replaces *A. silvestris*. The same applies to some young polyploid species, formed by hybridization followed by doubling of the number of chromosomes. According to J. Clausen ('Cytological evidence for the hybrid origin of *Penstemon neotericus* Keck', Hereditas, XVIII, pp. 65–76: 1933) the octoploid species *Penstemon neotericus* Keck ($n=32$) presumably originated in this way from two other Californian species with lower numbers (*P. laetus* ($n=8$) and *P. azureus* ($n=24$)). This presumably younger species has a small area, sharply contrasting with the wide and irregular areas of the putative ancestral species; it was probably formed in a place where these areas overlap, and had advanced northward, beyond the range of *P. laetus* and *P. azureus*.

Professor Weiss commented on the interest of Colonel Stern's communication as confirming Dr. Manton's observations that tetraploid species, with their apparently greater vigour, were likely to have a wider geographical distribution. He hoped that similar observations would be made on other genera of plants.

As regards the examples mentioned by Dr. M. Skalińska of the Anemone and *Penstemon*, in which certain tetraploid species showed a more limited range of distribution, these would be explained by Dr. Willis's 'Age and Area' theory as being species which had arisen comparatively recently.

PROCEEDINGS OF THE GENERAL MEETING
11 March 1943

held jointly with The Zoological Society of London

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 25 February 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting:—Mr. Frederick Chapman, Miss Fearson, Mr. A. Mayfield, Dr. E. S. Russell and Dr. Maria Skalińska.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted,—Major Brian Pollard-Urquhart.

The following candidates were balloted for and elected Fellows,—in favour of Dr. Raphael Ernest Grail Armattoe, M.Litt., Capt. James Percy Tufnell Burchell, M.C., Emlyn Glyndwr Davies, Michael Curtis Rawlence and Dr. John Smart.

The President reported the deaths of the following Fellows,—Mr. J. Graham Murray and Mr. A. W. Bartlett.

The proposed Alterations in the Bye-Laws were read from the Chair for the second time.

The President made the following statement :—In putting forward the proposed lowering of the Composition Fee for Fellows of twenty years' standing or over who have reached the age of sixty-five, the Council's intention is to help those Fellows to remain in the Society after they have retired from active life. The option to pay the Composition Fee of £20 in five annual subscriptions has the same object in view. The payment of this Composition Fee, either in full or by subscriptions, will be dated from the time a Fellow of sixty-five years or over applies to compound ; the previous payments of Annual Contributions will not be ranked as part-payments of the Composition Fee. In the event of a Fellow dying before the completion of the payment of the five annual subscriptions, the Council does not intend to claim the unpaid subscriptions from his executors.

Dr. Malcolm A. Smith exhibited a specimen of the Mexican Loggerhead Turtle (*Caretta kempi*) which had been stranded at Polzeath, near Padstow, Cornwall, on 3 January 1943. He pointed out the chief characters which distinguish it from the Atlantic Loggerhead (*Caretta caretta*) and drew attention to the fact that all the specimens of either species known to have reached this country had done so in the winter months of December and January.

The President referred to modern views about the Gulf Stream and its circulation of waters in the north Atlantic, and expressed the opinion that the turtle had been carried across by the NE. drift current which is caused by the prevailing south-westerly winds. Possibly the circumstances of strandings in winter might be accounted for by the increased strength of these winds at that season.

Mr. I. A. Williams asked if the turtle had arrived alive, to which Dr. M. A. Smith replied that he believed so.

The following communications were read and discussed :—

Theodore H. Savory, M.A. An account of the British Harvestmen (Opiliones). This is the first of a series of the Synopses of the British Fauna. Other sections are in course of preparation. (Communicated by Mr. D. M. Reid. Discussed by the President, Dr. E. Marion Delf and Miss R. F. Shove.) [Printed in full below.]

Dr. T. A. Sprague. Field studies on *Valeriana officinalis* Linn. in the Cotswold Hills. (Discussed by Dr. Maria Skalińska, Mr. W. C. Worsdell and Canon F. W. Galpin.) [Printed in full, p. 93.]

SYNOPSES OF THE BRITISH FAUNA—No. 1. OPILIONES.

By Theodore H. Savory, M.A., F.Z.S.

The British Harvestmen have several features which should recommend them to naturalists for study. There are only twenty species ; fourteen of them are probably to be found in every county, and twelve of them can be named at a glance. It is the purpose of this paper to show how they may be identified, to summarize the scanty records of their occurrence and to show that any collector can help in completing our knowledge of their distribution.

The Order Opiliones includes about 2,000 species, divided among three sub-orders. Only one of these, the Palpatores, is British. It contains six families, three of which are British—the Trogulidae (two species), the Nemastomatidae (two species) and the Phalangiidae (sixteen species). These figures are given because they show that British Harvestmen represent but a restricted fraction of the world's population ; and, in fact, the biology of many foreign species is very different from that of our own.

Structure.—Some knowledge of the structure of the Harvestmen is necessary to enable one to understand their mode of life and to use the identification key. The Opiliones are an Order of the Class Arachnida, in which their most familiar relatives are the spiders, scorpions and mites. They differ from spiders most obviously in having no waist, the two portions of the body, cephalothorax and abdomen, being joined across their whole breadth. The shape of the body is usually a smooth oval, and the only traces of segmentation are transverse grooves or rows of tubercles.

On the cephalothorax there are two eyes which in all common British species are large and are set back to back on an eminence. In the forepart there is a pair of odoriferous glands which open near the bases of the second legs. There are six pairs of appendages—chelicerae, pedipalpi and four pairs of legs.

The chelicerae have three segments each, the last segment works against a projection of the second, forming a pincer-like limb, quite different from the piercing jaws of spiders, and containing no poison-glands.

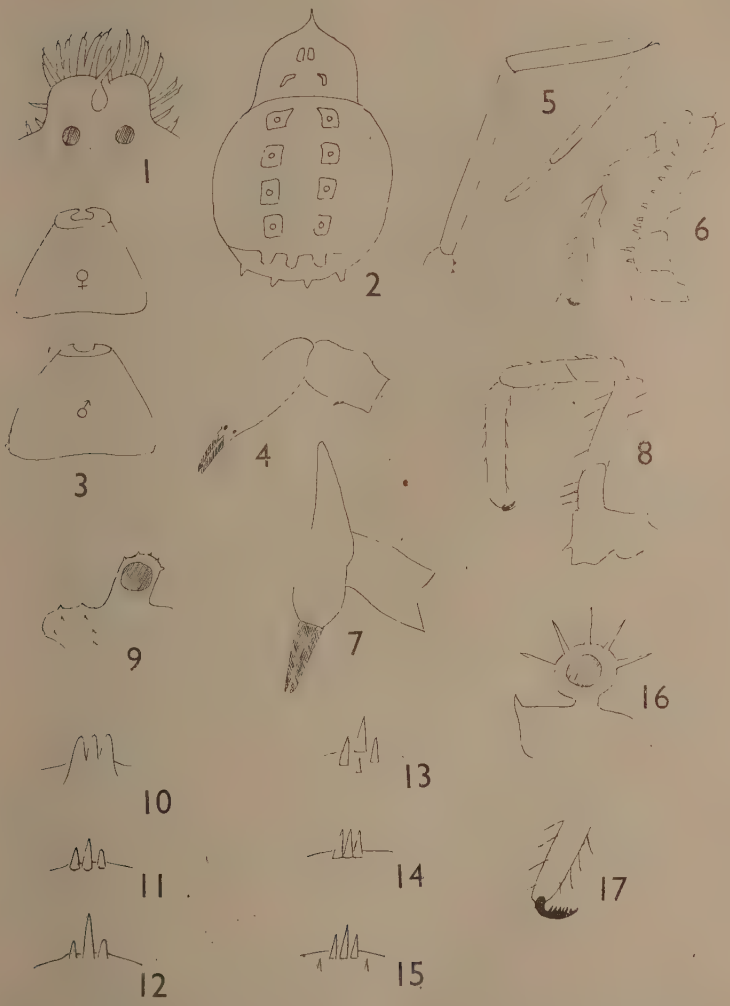
The pedipalpi or palpi are leg-like and are composed of six segments. The legs have seven segments—coxa, trochanter, femur, patella, tibia, metatarsus, tarsus. It is the metatarsus that is missing from the pedipalp. The tarsi of the legs are usually broken up into a large number of pieces, all bearing setae and forming a whip-like, sensitive limb.

The sexes are not usually very different : males have often smaller bodies and longer legs than females.

Most British Harvestmen are nocturnal in their habits, although a few species may occasionally be found running about in the autumn sunshine. Their diet appears to be varied. Undoubtedly they sometimes capture living prey, but they are also known to feed on dead animals, and have been seen to take the sugar spread to catch moths, and even the marmalade at a human picnic. In captivity they accept a wide range of food. They also require water to drink, and cannot be kept alive in cages without it.

Unlike spiders, they show no preliminary courtship actions, but mate freely and unhesitatingly when the sexes meet. The eggs are laid in clusters of about thirty at a time below the surface of damp soil. Most species appear to lay their eggs in the autumn. The young are hatched in the spring or early summer, but two or three species may be found as adults throughout the year.

Very little ecological observation has been recorded about Harvestmen. The genus *Nemastoma* reaches the summits of the highest mountains in Britain, and the variety of *Mitopus morio* known as *alpinus* seems only to occur at considerable heights. The family Trogulidae apparently



1, Hood of *Anelasmocephalus cambridgei*. 2, Outline of *Homalenotus quadridentatus*, showing spine in front of cephalothorax and four blunt processes on abdomen. 3, Genital plate of female and male *Oligolophus agrestis*. 4, Chelicera of *Mitopus morio*, showing ventral spur on proximal segment. 5, Palp of *Nemastoma chrysomelas*; short tarsus without claw. 6, Palp of *Odiellus meadi*; long tarsus with claw, teeth on femur. 7, Chelicera of male *Phalangium opilio*, showing dorsal horn on second segment. 8, Palp of *Oligolophus agrestis*; setae on femur. 9, Backwardly directed ocularium of *Mitopus*. 10, Trident of *Odiellus spinosus*. 11, Trident of *Odiellus palpinalis*. 12, Trident of *Odiellus meadi*. 13, Trident of *Oligolophus agrestis*. 14, Trident of *Oligolophus tridens*. 15, Trident of *Oligolophus hanseni*. 16, Ocularium of *Megabunus diadema*. 17, Toothed palpal claw of Liobuninae.

lives only on a chalk soil. For the rest, distribution is much more general, and the normal habitat is a ditch or a wood or any spot where fallen leaves accumulate. As an example, eleven species have been found in one afternoon in one lane in Hertfordshire, which shows that most of our species seek the same kind of environment.

Like other Arachnida, Harvestmen grow by periodic casting of the exoskeleton. The number of such moults occurring between birth and maturity appears not to have been determined. The young are very difficult to rear.

Limbs are freely shed by autotomy, but are not regenerated at moulting, a remarkable feature which seems to be peculiar to the Order.

List of British Opiliones.

Family TROGULIDAE.

Trogulus tricarinatus (Linnaeus).
Anelasmocephalus cambridgei (Westwood).

Family NEMASTOMATIDAE.

Nemastoma lugubre (Müller).
Nemastoma chrysomelas (Hermann).

Family PHALANGIIDAE.

Subfamily Sclerosomatinae.

Homalenotus quadridentatus (Cuvier).

Subfamily Liobuninae.

Liobunum rotundum (Latreille).
Liobunum blackwalli Meade.
Nelima silvatica (Simon).

Subfamily Oligolophinae.

Mitopus morio (Fabricius).
Oligolophus tridens (C. L. Koch).
Oligolophus agrestis (Meade).
Oligolophus hanseni (Kraepelin).
Odiellus palpinalis (Herbst).
Odiellus spinosus (Bosc).
Odiellus meadi (Cambridge).
Lacinius ephippiatus (C. L. Koch).

Subfamily Phalangiinae.

Phalangium opilio Linnaeus.
Opilio parietinus (De Geer).
Platybunus triangularis (Herbst).
Megabunus diadema (Fabricius).

Family TROGULIDAE.

The two species which represent this family in Britain are among the rarest of our Arachnida, though the 'rarity' is due to their limited

range and retiring habits. The characteristics of the family, which make it easily recognizable, are three. First, the legs are comparatively short and their tarsi consist of 2, 2, 3, 3, segments only. Secondly, there is no tubercle carrying the eyes, which are set on the surface of the carapace, like the eyes of spiders. Thirdly, and most characteristic, the fore-edge of the carapace is produced forwards into a bifurcated hood, under which the chelicerae and mouth-parts are hidden. The two species are not difficult to distinguish.

Trogulus tricarinatus (Linn.). (Syn. *T. asperatus*, *T. rostratus*.)
Length 7 mm.

In this species the hood is composed of large semicircular plates which meet, or nearly meet, in front and which are furnished on their outer edge with short cylindrical tubercles, each surmounted by a spine or seta. The colour is brown in the adult, but the young are a striking purple.

Distribution.—Cornwall, Dorset, Kent, Surrey, Derby.

Anelasmocephalus cambridgei (Westw.).
Length 3·5 mm.

In this species the hood is composed of smaller plates with much longer cylindrical tubercles, armed with spines (fig. 1). This distinction, together with the smaller size of the adult, sufficiently characterizes the species.

Distribution.—Cornwall, Dorset, Hampshire (Isle of Wight), Sussex, Kent, Surrey, Derby, Warwickshire, Glamorgan, Denbigh.

Family NEMASTOMATIDAE.

The two British members of this family are superficially so unlike that it is not easy to believe that they should be placed in the same genus. Besides the absence of the anterior hood and the presence of an ocular tubercle, which separate all remaining British Harvestmen from the Trogulidae, the Nemastomatidae possess palpi in which the tarsus is much shorter than the tibia and has no terminal claw (fig. 5). The coxae of the legs are strongly and characteristically toothed on their edges; those of the first, but not the second, pair possess gnathobases. The abdomen shows segmentation much more clearly than in any other British species.

Nemastoma lugubre (Müller). (Syn. *N. bimaculatum*.)
Length 2·3 mm.

This common species is wholly black, save for two large white or pale yellow spots on the cephalothorax. The legs are quite short. This species and the next reach the tops of the highest mountains in Great Britain, and are generally distributed all over the kingdom.

Nemastoma chrysomelas (Hermann).
Length 2·5 mm.

The legs of this species are longer than those of the above. The animal is an almost uniform brown colour with transverse lines of small tubercles marking the abdominal segments. It is at once recognizable

by its pedipalpi, which are much longer than its body (fig. 5) and are armed with characteristic knobbed spines. It occurs under fallen leaves at all times of the year, even mid-winter.

Distribution.—Devon, Dorset, Surrey, Norfolk, Staffordshire, Lancashire, Yorkshire, Northumberland, Cumberland. Also in Scotland (Inverness) and Ireland (Carlow).

Family PHALANGIIDAE.

In this family, which includes the remaining sixteen British species, the tarsal segment of the pedipalp is longer than the tibial, and ends in a claw. The legs of the second pair, which are always the longest, bear gnathobases on their coxae.

Subfamily Sclerosomatinae.

In this group the exoskeleton is much firmer than in the other subfamilies, and carries four large pointed tubercles on its posterior margin. This is really the fifth abdominal segment, the remaining segments being bent down at right angles, forming a 'sternwalk' and surrounding the anus. A fifth pointed tubercle is situated in the middle of the fore-edge of the cephalothorax (fig. 2).

Homalenotus quadridentatus (Cuvier). (Syn. *Sclerosoma romanum.*)
Length 5 mm.

This, the only British species, is unmistakable because of its clear abdominal pattern of four rows of four dark spots, on each of which is a small blunt tubercle.

Distribution.—Wiltshire, Dorset, Sussex, Surrey, Hertfordshire, Buckinghamshire, Worcestershire, Herefordshire.

Subfamily Liobuninae.

This subfamily contains three British species, in which the legs are excessively long and the abdomen, especially in the males, is small and sometimes almost circular, with its segmentation almost invisible. The palpal claw is toothed (fig. 17) (as in the Sclerosomatinae). The females normally show a pattern on the abdomen, consisting essentially of a darker median area, while the males are uniformly brown, or nearly so. Two species are very common, and the third has so far been recorded once only.

Liobunum rotundum (Latreille).
Length, ♀ 6 mm., ♂ 3·5 mm.

The long legs of this species, which are dark brown or nearly black, have no spines, but only very small denticles on the femora. The eyes, on a smooth tubercle, are each surrounded with a clear black ring.

Distribution.—Cornwall, Devon, Somerset, Wiltshire, Dorset, Hampshire, Surrey, Essex, Hertfordshire, Oxfordshire, Norfolk, Cambridgeshire, Worcestershire, Staffordshire, Shropshire, Cheshire, Yorkshire, Durham. Also in Wales and Ireland.

LIOBUNUM BLACKWALLI Meade.
Length, ♀ 6 mm., ♂ 3·4 mm.
This species closely resembles the above, but is at once distinguishable by a white ring surrounding each eye.
Distribution.—Devon, Dorset, Surrey, Hertfordshire, Worcestershire. Also in Ireland.

NELIMA SILVATICA (Simon).
Length, ♀ 3·5 mm., ♂ 2·5 mm.
This species has only once been recorded from the mainland, a male having been found at Minehead by Dr. A. R. Jackson in 1938. It had previously been found on the islands of Skokholm and Moy, but it is possible that it occurs elsewhere near the shore. It superficially resembles *L. blackwalli*, but has pale trochanters and a dark spot on the coxae.

Subfamily OLIGOLOPHINAE.

This subfamily may be recognized by two features, viz., the presence of a small ventral spur on the first segment of the chelicerae (fig. 4) and a conspicuous trident of three large spines on the cephalothorax in front of the ocular tubercle. It contains eight species distributed among four genera. Three of the eight may be reckoned as being among the 'unmistakables', but a little care is needed in distinguishing the others. The features of the genera are :—
Mitopus.—The spines of the trident are quite small, uniform in size and relatively far apart.
Oligolophus.—The trident is conspicuous, and the palpal femora carry simple black spines below (fig. 8).
Odiellus.—The palpal femora strongly toothed (fig. 6) ; the femora and patellae of the legs with simple spines below ; leg-segments with terminal spurs.
Lacinius.—The femora of palpi and of legs with strong teeth, surmounted with spines.

MITOPUS MORIO (Fabricius). (Syn. *Oligolophus palliatus* ; *O. alpinus* ; *O. cinerascens.*)
Length, ♀ 7 mm., ♂ 5 mm.
The pattern on the back of this species is a black mark, constricted in the middle, and broadening towards the eyes and anus so that it has somewhat the shape of an hour-glass. The legs are longer than in *Oligolophus* and are lighter in colour. The species is widespread and often plentiful. An upland variety has been described under the name of *O. alpinus* : it differs from the typical form in having the third metatarsi curved and thickened, but the females appear to be indistinguishable.
Distribution.—All over England ; also in Scotland, Wales and Ireland. On small islands and on mountains.

LACINIUS EPHIPPIATUS (C. L. Koch). (Syn. *Oligolophus vittiger.*)
Length, ♀ 6 mm., ♂ 4 mm.
This is a very distinct species : the ground colour is a pale yellow-brown and the central mark, which is black, has parallel straight sides and is

squarely cut off at its posterior end, some way from the abdominal margin.

Distribution.—Wiltshire, Dorset, Surrey, Essex, Hertfordshire, Oxfordshire, Norfolk, Cambridgeshire, Worcestershire, Staffordshire, Cheshire, Yorkshire. Also in Scotland and Wales.

ODIELLUS SPINOSUS (Bosc). (Syn. *Opilio histrix*.)

Length, ♀ 9 mm., ♂ 7 mm. Breadth 5 or 6 mm.

The shape of the body of this species is like that of no other British Harvestman; it is flat and broad, like that of a crab-spider, and the animal is much bulkier than any other. The spines of the trident point almost horizontally forward and arise from a small, readily-separable area (fig. 10).

Distribution.—Dorset, Hampshire, Kent, Surrey, Middlesex, Hertfordshire, Oxfordshire, Cambridgeshire, Northamptonshire, Gloucestershire, Worcestershire, Warwickshire, Leicestershire.

ODIELLUS PALPINALIS (Herbst). (Syn. *Phalangium terricola*.)

Length, ♀ 5 mm., ♂ 4 mm.

In this species the spines of the trident are almost vertical and are set in a straight line, the central spine being slightly longer than its neighbours (fig. 11). The patella of the palp has a slight distal apophysis and the legs are ringed with brown. It is similar to but smaller than *Oligolophus tridens*, from which the spines, mounted on tubercles on the palpal tibia, will readily distinguish it.

Distribution.—Dorset, Surrey, Middlesex, Norfolk, Staffordshire, Cheshire, Yorkshire. Also in Scotland.

ODIELLUS MEADI (Cambridge).

Length, ♀ 4 mm., ♂ 3 mm.

The spines of the trident in this little species are in a straight line and point forwards, the central spine being at least twice as long as its neighbours (fig. 12). The tarsal joints of the legs have conspicuously long setae, and a more obvious character is the demarcation of the abdominal segments by transverse rows of strong denticulae.

Distribution.—Dorset, Sussex, Kent, Cheshire.

OLIGOLOPHUS TRIDENS (C. L. Koch).

Length, ♀ 6 mm., ♂ 4 mm.

This species and the next are among the commonest and most widely distributed British species. Its trident consists of three spines in a straight line (fig. 14), and its other distinguishing features are its angular femora and its smoothly rounded genital plate.

Distribution.—General; also in Scotland, Wales and Ireland.

OLIGOLOPHUS AGRESTIS (Meade). (Syn. *O. ephippiger*.)

Length, ♀ 6 mm., ♂ 4 mm.

This species is distinguishable from the foregoing by its occasional reddish colour, rounded femora and a conspicuous notch in the front of the genital plate (fig. 3). The central spine of the trident is slightly the longest and is a little in advance of the others (fig. 13).

Distribution.—General; also in Scotland (Sutherland), Wales and Ireland.

OLIGOLOPHUS HANSENI (Kraepelin).

Length, ♀ 6 mm., ♂ 4 mm.

The trident of this species, which is a straight line, has the central spine the longest and, in addition, there is a spine on each side of the trident and a group of six behind it (fig. 15). The femora are cylindrical and the genital plate is smoothly rounded in front.

Distribution.—Surrey, Warwickshire, Shropshire, Cheshire, Yorkshire. Also in Scotland.

Subfamily PHALANGIINAE.

The features which distinguish this subfamily are the absence of the ventral spur on the chelicerae and the absence of the trident of anterior spines. Of greater practical importance, however, is the fact that each of the four species which it includes is individually recognizable by conspicuous characters of its own.

PLATYBUNUS TRIANGULARIS (Herbst). (Syn. *P. corniger*.)

Length, 5 mm.

This is a yellow-brown species which appears in Britain in the spring and early summer, some weeks before most of the others. It bears a slight superficial resemblance to *Phalangium opilio*, but the branch on the tibia of the palp distinguishes it at once.

Distribution.—Cornwall, Devon, Wiltshire, Dorset, Hampshire, Surrey, Oxfordshire, Norfolk, Worcestershire, Warwickshire, Staffordshire, Shropshire, Cheshire, Yorkshire, Durham. Also in Scotland (Perth, Argyll and Inverness) and in Ireland.

MEGABUNUS DIADEMA (Fabricius). (Syn. *M. insignis*.)

Length, 4 mm.

This beautiful little animal is also an early species and is often to be found on hills where other species are absent. On its abdomen there is an intricate pattern of green, silver and black, but its most remarkable feature is its ocular tubercle. This carries two rows of five very long sharp spines, making a conspicuous object unlike anything else among the British species (fig. 16).

Distribution.—Devon, Wiltshire, Dorset, Hampshire, Surrey, Norfolk, Worcestershire, Warwickshire, Staffordshire, Shropshire, Cheshire, Lancashire, Yorkshire, Durham. Also in Scotland (Perth and Inverness) and Ireland.

PHALANGIUM OPILIO Linnaeus. (Syn. *P. canescens*, *P. cornutum*, *P. brevicorne*, *P. molluscorum*.)

Length, ♀ 9 mm., ♂ 7 mm.

This is the common conspicuous Harvestman of autumn, and is one of the largest of our species. Its abdomen is yellow-brown, usually with a dark streak in the centre. The chelicerae of the male give immediate identification of the species in this sex; the second segment is produced upwards into a conical horn (fig. 7). A feature of both sexes is that the whole of the lower surface of the body is white.

Distribution.—Throughout England; also recorded from Scotland (Perth and Sutherland), Wales and Ireland.

Opilio parietinus (De Geer). (Syn. *Phalangium cinereum*, *P saxatile*.)

Length, ♀ 7 mm., ♂ 5 mm.

This species, which is the latest of the British Harvestmen to come to maturity, has a characteristic mottled grey pattern with a narrow brown streak, or a row of brown dots, down the centre of the abdomen. The lower surface is pale and each coxa carries a dark oval spot.

Distribution.—Devon, Wiltshire, Dorset, Kent, Surrey, Essex, Hertfordshire, Middlesex, Oxfordshire, Norfolk, Cambridgeshire, Herefordshire, Worcestershire, Staffordshire, Shropshire, Cheshire, Lancashire, Yorkshire. Also in Scotland (Lanark) and in Ireland.

Dichotomic Table for British Opiliones.

1	(4).	Cephalothorax with bifurcated hood; eyes level with surface of carapace (Fam. Trogulidae) ..... 2.
2	(3).	Hood of large semi-circular plates, with small tubercles on outer edge ..... *Trogulus tricarinatus*.
3	(2).	Hood of small projections, with long cylindrical tubercles ..... *Anelasmocephalus cambridgei*
4	(1).	No such hood; eyes raised on ocularium.... 5.
5	(8).	Tarsus of pedipalp without claw (Fam. Nemastomatidae) ..... 6.
6	(7).	Body black with two white spots; palpi of normal length ..... *Nemastoma lugubre*.
7	(6).	Body yellow-brown; palpi much longer than body ..... *Nemastoma chrysomelas*.
8	(5).	Tarsus of pedipalp with claw (Fam. Phalangiidae) ..... 9.
9	(16).	Palpal claw toothed..... 10.
10	(11).	Abdomen with four conspicuous tubercles on posterior margin (subfam. Sclerosomatinae); four rows of dark spots on upper surface ..... *Homalenotus quadridentatus*.
11	(10).	Abdomen smooth posteriorly; legs exceedingly long (subfam. Liobuninae) ..... 12.
12	(15).	Ocular tubercle smooth; trochanters dark; coxae without dark spot (genus *Liobunum*). 13.
13	(14).	Black ring round eyes ..... *Liobunum rotundum*.
14	(13).	White ring round eyes ..... *Liobunum blackwalli*.
15	(12).	Ocular tubercle with two rows of teeth, trochanters pale; coxae with dark spot .. *Nelima silvatica*.
16	(9).	Palpal claw smooth ..... 17.
17	(32).	First segment of chelicerae with ventral spur; ante-ocular region with trident of three spines (subfam. Oligolophinae)..... 18.
18	(15).	Femora of palpi with ventral spines or teeth. 19.
19	(20).	Femora and tibiae of legs strongly toothed .. *Lacinius ephippiatus*.
20	(19).	Femora and tibiae of legs only hairy ..... 21.
21	(22).	Body broad and flat; trident spines almost horizontal ..... *Odiellus spinosus*.
22	(21).	Bodily proportions more normal; trident spines erect or nearly so ..... 23.
23	(24).	Central spine of trident slightly longest; palpal patella with apophysis ..... *Odiellus palpinalis*.
24	(23).	Central spine of trident twice as long as the others; setae on tarsi long ..... *Odiellus meadi*.
25	(18).	Femora of palpi ventrally only hairy..... 26.

26 (27). Fore-edge of carapace with trident of small tubercles; legs long ..... *Mitopus morio.*
27 (26). Fore-edge of carapace with 1–3 spines; legs not very long ..... 28.
28 (29). Central spine of trident slightly longest and in advance of others; genital plate with anterior notch ..... *Oligolophus agrestis.*
29 (28). Spines of trident in straight line ..... 30.
30 (31). Angular femora; light colour ..... *Oligolophus tridens.*
31 (30). Cylindrical femora; dark colour..... *Oligolophus hanseni.*
32 (17). No spur on chelicerae; no trident on carapace (subfam. Phalangiinae) ..... 33.
33 (36). Tibial joint of palp with apophysis..... 34.
34 (35). Ocular tubercle with two rows of five long spines ..... *Megabunus diadema.*
35 (34). Ocular tubercle with normal spines ..... *Platybunus triangularis.*
36 (33). Tibial joint of palp unbranched ..... 37.
37 (38). Brown species with dark central mark; second joint of male chelicera with horn .. *Phalangium opilio.*
38 (37). Grey species with row of brown dots in centre *Opilio parietinus.*

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Discussion.—

The PRESIDENT congratulated Mr. Savory on his interesting account of this little-known group. He informed the meeting that Mr. Savory had prepared his valuable key to the British species of Opiliones at the instance of the Crustacea Committee of the Society, and that the Society intended to publish it as the first of a series of ecological fauna lists to be sponsored by its sectional committees.

Dr. E. M. DELF said that she had mostly noticed Harvestmen running over dry ground in late summer, that is to say by no means in the vicinity of water, and she asked if there is a period in their lives when the need of water is in abeyance, or is it that in some species the need is less pronounced?

Miss R. F. SHOVE asked if the marked need of water could be easily accounted for?

Mr. SAVORY answered that he had no theory to put forward in regard to water requirements.

FIELD STUDIES ON VALERIANA OFFICINALIS LINN. IN THE COTSWOLD HILLS.

By T. A. Sprague.

The area explored is roughly bounded by an irregular quadrilateral, with Cheltenham, Stroud, Cirencester and Andoversford as the corners, and Colesbourne as the centre. Herbarium specimens of about 200 plants from 30 to 40 different localities were collected.

Drabble (1933) distinguished three species of *Valeriana* belonging to the *officinalis* group in Britain, namely *V. angustifolia* Host, *V. officinalis* Linn. (with two forms, *dentatifolia* Druce and *latifolia* Vahl), and *V. sambucifolia* Mikan. War-time conditions limit opportunities of consulting types and original descriptions ; but it may be observed parenthetically that the British forms named *angustifolia* and *sambucifolia* by Drabble and others are not quite identical with the Continental forms described under these names, judging from herbarium specimens and descriptions in 'floras'. For example, *V. angustifolia* Host, as represented by Fl. Exsicc. Austr.-Hung. n. 3445 (Herb. Kew), has more numerous leaflets than have British plants so named, and *V. sambucifolia* Mikan, as described by Hayek and Hegi (1914) and by Schinz and Thellung (1923), has the soboles above ground, in contrast to the corresponding British forms, in which they are below ground.

The principal characters of the three species given by Drabble are as follows :—

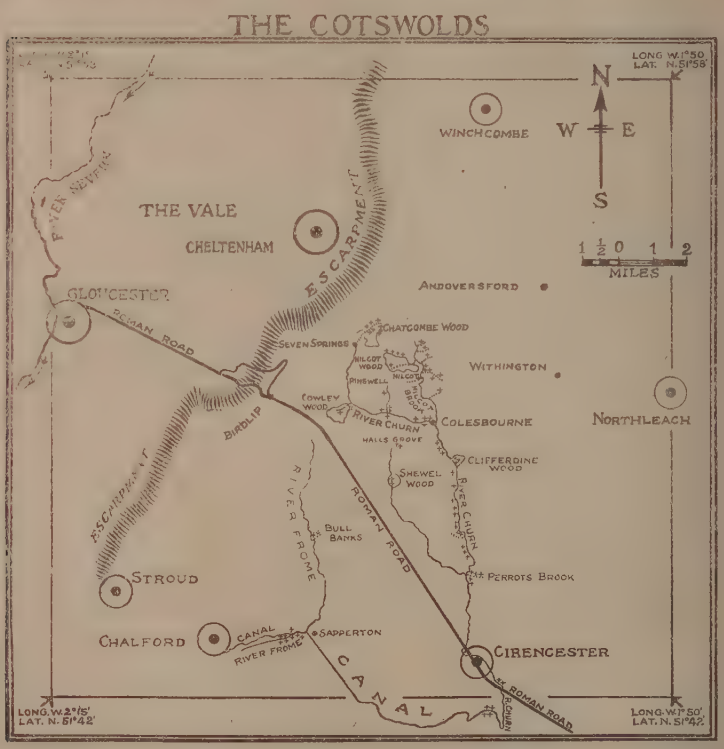
(i) *V. angustifolia* : lateral leaflets 7–9 pairs, those of the lower leaves narrow, linear-oblong, parallel-sided, obtuse, entire, scarcely narrowed to the base, strongly decurrent, those of the stem-leaves narrowly linear-lanceolate, acute or subacute, entire (or rarely with a few teeth), narrowed at each end, sessile, decurrent, terminal leaflet little or not at all broader than the others ; stolons usually short or absent.

(ii) *V. officinalis* : lateral leaflets 7–8 pairs, ovate-lanceolate to linear-lanceolate, acute or acuminate, narrowed to the base, all toothed, usually more abundantly on the basiscopic margin, acroscopic margin sometimes entire, terminal leaflet not much larger than the others, often no larger, acute ; stolons usually short.

(iii) *V. sambucifolia* : lateral leaflets 3–5 pairs, broadly lanceolate or ovate, toothed on both margins, terminal leaflet larger than the others and with very broadly rounded apex which bears large teeth of which the uppermost are often as long as, or nearly as long as, the apex, which is usually obtuse ; stolons long.

Certain plants found in the Cotswold Hills agree fairly well with Drabble's descriptions of the three species, but the specimens, as a whole, form a more or less continuous series, comprising many different forms. The differences between these appear to be almost entirely vegetative, including such characters as the number of leaflets, their shape, size, texture, colour, amount of decurrence on the rhachis, the degree of toothing and position of the teeth, the length of the partial internodes separating the pairs of leaflets, and the shape and size of the terminal leaflet relatively to the lateral ones. The problem is complicated by the

fact that the successive leaves of a single individual show a great range in these characters (see p. 96). Drabble includes in his descriptions characters drawn from the fruit; but these do not seem to hold good. Differences in the size of the corolla occur, but these are apparently not correlated with the vegetative characters, though plants of the *sambucifolia* type seem to have rather larger flowers on the whole.



Map of the area explored. A broken line indicates the bottom of a dry valley; crosses, the localities of *Valeriana officinalis*.

As may be gathered from Drabble's descriptions, there are greater morphological differences between typical *sambucifolia* and *officinalis* than between typical *officinalis* and *angustifolia*. This is reflected in the frequent division (or sub-division) of *V. officinalis* Linn. into two species (or subspecies), *officinalis* and *sambucifolia*. *V. angustifolia* seems to be merely an extreme state of *V. officinalis* found in relatively dry and sunny habitats.

Topographical distribution and habitats.—The distribution of *V. officinalis* in the Cotswold Hills follows the valleys of the rivers and streams, and the small dry valleys which run into the larger watered ones. It appears

to be absent from the flat ground on the top of the hills, except along the margins of woods which extend up from the dry valleys. The basin of the river Churn may be taken as an example. The Churn runs roughly southwards and south-east from Seven Springs past Cirencester to the neighbourhood of Cricklade, where it joins the Thames. *V. officinalis* occurs at various points by the side of the Churn from Cockleford to Perrott's Brook, under isolated alder trees, and where there is woodland on one side of the river. It also grows on the grass verges and banks of the Cheltenham Cirencester road, which runs parallel to the Churn, about 200 yards away or less. It is found also in the tributary valleys leading to Chatcombe Wood (dry valley), Cowley Wood, and Pinswell Plantation, and the valleys of the Hilcot Brook and Perrott's Brook (at Shewel Wood), as well as in minor dry valleys leading upwards from Rendcomb and the hamlet of Perrott's Brook. Most of the lower course of the Hilcot Brook is too densely wooded for its occurrence, but it is found in more open woodland along the road parallel to and close to the upper part of the Hilcot Brook, as well as in at least six dry lateral valleys. Further stations for *V. officinalis* are in the valley of the river Frome, and by the disused Thames–Severn canal, near Sapperton and near South Cerney.

Various types of habitat may be distinguished: on river banks, and on flat stretches of land beside streams, and by canals; on the margins of woods, and along woodland tracks and glades; in pure ash woods; on grass verges and banks by roadsides; and on downland slopes. In all cases the habitats are such as afford a moderate amount of shade, or, at least, protection from direct sunlight during part of the day. On river banks *V. officinalis* frequently occurs under alder trees, and along roadsides partial shade may be afforded by steep hedge-crowned banks, or by woods on one or both sides. Even on comparatively open slopes it does not grow far from trees or shrubs.

Influence of the environment on the vegetative characters.—Plants in damp shady places approach the *sambucifolia* type, and those in light woodland the *officinalis* type, while those on rather sunny slopes exhibit a considerable range of forms connecting the *officinalis* and *angustifolia* types. A fairly complete series of vegetative types ranging from *sambucifolia* almost to *angustifolia* has been found in a variety of habitats in the Sapperton valley, and a series including many forms linking *officinalis* and *angustifolia* has been collected in a narrow dry valley running up from the Hilcot Brook eastwards from Lower Hilcot along the Withington road. The profusion of different forms in the latter valley, many of them growing in apparently identical environments, suggests that at least some of the forms have a genic basis. Similar but smaller ranges of forms have been found in other localities, without any apparent differences in environment, as on a grass verge at Marsden, and at the edge of Mercombe Wood.

A peculiar form that might be assigned to the *sambucifolia* type has been found only in an alder-ash copse at the south-west corner of Hilcot Wood, close to a permanent spring near which *Chrysosplenium oppositifolium* Linn., *Allium ursinum* Linn. and *Caltha palustris* Linn. were growing in very spongy soil. This has lanceolate lateral leaflets, hardly

toothed on the acroscopic margin, and links up with forms from an ash wood at Chescombe, with more numerous and still narrower leaflets, that might be assigned to the *officinalis* type. The Chescombe plants, in their turn, form a transition to a single plant found under ash trees in a wood east of Lower Hilcot, which forms one end of a series leading to the *angustifolia* type.

On the whole, it seems that plants of *V. officinalis* in the shade produce larger, relatively broader, and more toothed leaflets than those in sunny spots nearby. This is illustrated by plants of the *sambucifolia* type growing in different degrees of shade by the river Churn below Colesbourne Inn. Similar differences are observable among plants of the *officinalis* type growing by the road leading from Upper Hilcot to the Seven Springs–Andoversford road. Transplant experiments are required to test the influence of environment on the various forms. In the meantime, caution in using the relative breadth and toothing of the leaflets as taxonomic characters is suggested by the great differences sometimes observable between the successive leaves of young plants in the year before they flower. On the same individual, collected in the autumn, there may be a transition from the oldest leaf, with 9 pairs of narrow leaflets, which are entire, or only slightly toothed on the basiscopic margin, to the youngest, with 6–7 pairs of broad leaflets, coarsely toothed on both margins.

Certain plants which at first sight appear to be distinct forms are probably starvelings in which all the cauline leaves are like the upper leaves of vigorous plants growing near them, e.g. two extremes found by the disused Thames–Severn canal near South Cerney. Such weak slender-stemmed plants often have narrower and less toothed leaflets than the corresponding vigorous ones, e.g. two plants by the river Churn south-east of Cirencester.

Distinct forms.—After allowance has been made for the influence of environment and the degree of nutrition, there remain about 15 to 20 apparently distinct forms, some of which are recognizable at a glance. A giant plant, about 6 ft. high, was discovered in marshy ground beside the river Frome at Sapperton by Mrs. Sprague, who suggested that it might be a polyploid. Dr. Skalińska, who has very kindly undertaken a cytological examination of various forms, finds that it is an octoploid, with 56 chromosomes (see below, p. 103). The giant represented an extreme development of the *sambucifolia* type, with cauline leaves up to 15 inches long, and leaflets up to 5 inches long, very coarsely toothed on both margins ; the lower bracts are foliaceous, and unifoliolate with a very coarsely toothed margin ; the leaves on the lateral branches resembled those on the main stem of a plant of the ordinary *sambucifolia* type. Another striking form of the *sambucifolia* type has been found only near the hamlet of Perrott's Brook : this has broad leaflets, with the successive pairs *overlapping* downwards.

An outstanding form, of the *officinalis* type, with a very short leaf-rhachis and numerous crowded linear-lanceolate, acuminate, sparsely toothed leaflets, has been found only in two localities, near Rendcomb and near Lower Hilcot. Another short-leaved form, with fewer and well separated pairs of leaflets, occurs on a flat stretch of marshy ground between the Perrott's Brook and Shewel Wood.

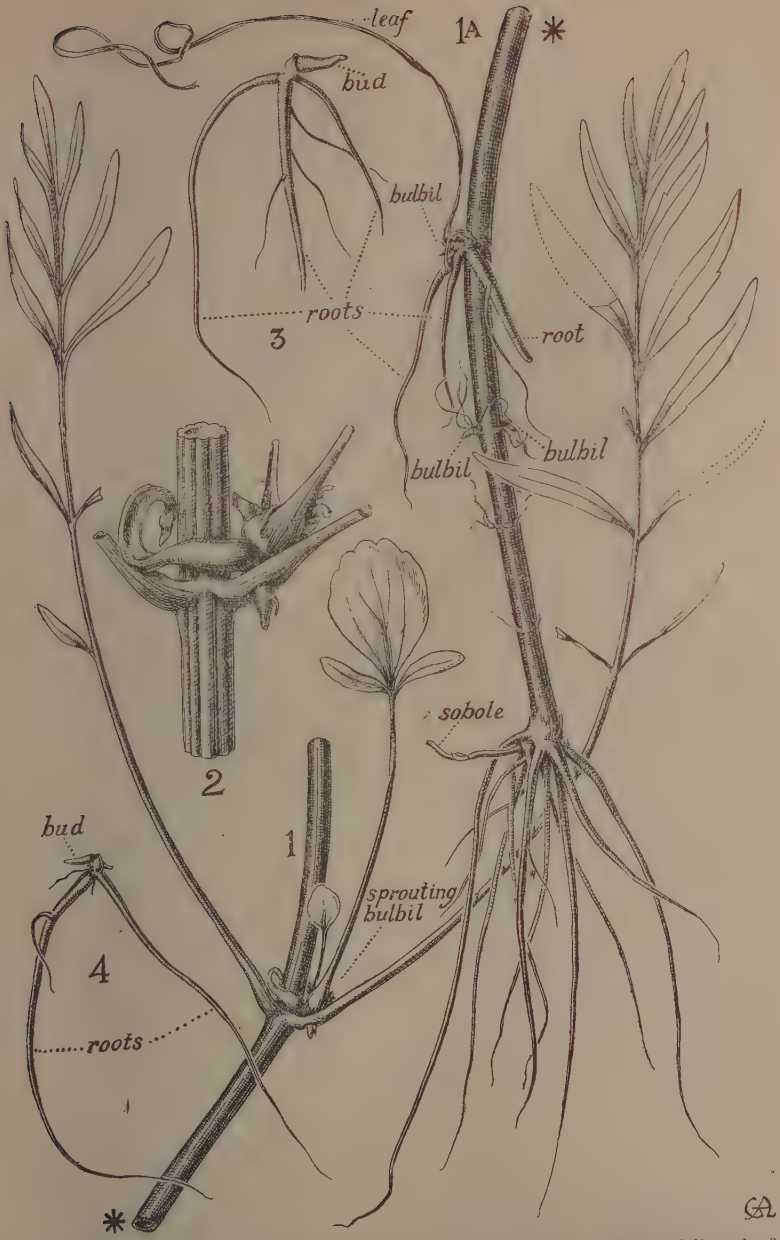


FIG. 1. —Middle part of plant, bearing a sprouting bulbil in the axil of a foliage leaf.
FIG. 1 A.—Lower part of plant, showing three bulbils in axils of decayed leaves, and a sobole.
FIG. 2. Node from 1.
FIGS. 3, 4.—Detached bulbils found on the ground at the base of the plant.

Figs. 1, 1 A, 3, 4, natural size; fig. 2, × 3.

Vegetative reproduction.—Two methods of vegetative reproduction have been observed in the Cotswold Hills:—(i) by underground runners or *soboles*, bearing scattered, sheathing, membranous scale-leaves arranged distichously, and rooting at one or more nodes to form separate plants; and (ii) by *bulbils*, which usually fall off the parent before sprouting. The flowering stem arises monopodially from a short premorse rhizome, at the base of which are the remains of the old sobole which gave rise to the rhizome, or the cicatrix left by it. The cicatrix exhibits two concentric circles, the inner corresponding to the ring of vascular bundles.

The soboles arise as lateral buds in the axils of decayed leaves at the base of the flowering stem, usually at or after flowering. In the Cotswold Hills the main flowering season of *V. officinalis* is July to August, and the soboles begin to develop well from August onwards. They may be very short, and the young plants then arise almost at the base of the flowering stem, or they may grow out several inches before rooting. The number given off by a flowering stem ranges from one to eight, as far as observed. The soboles root at one or more nodes to form one or more daughter plants. In vigorous individuals the old rhizome and the connection between it and the daughter plant or plants may persist until the following year, in both the *sambucifolia* and the *officinalis* types. In weak individuals the slender connecting soboles may decay and disappear.

The first leaves of a daughter plant have a single suborbicular or broadly ovate leaflet with a slightly undulate margin, and the next ones are usually trifoliolate, with a large terminal leaflet and a pair of smaller ones: as the plants grow older, leaves with an increasing number of leaflets are produced. An original daughter plant may, if vigorous enough, develop a flowering stem two years after the flowering of its parent plant. Fully grown vegetating plants, which would presumably have flowered in 1942, were collected in the late summer of 1941, attached by soboles to the rhizome of a plant which had flowered in 1940. The production of soboles is not confined to plants which have reached the flowering stage: vigorous young plants may, in the year before they flower, produce soboles and small daughter plants.

Thus far we have been dealing with the well-known phenomenon of large plants producing soboles which root to form smaller daughter plants, but the reverse process is just as common in *V. officinalis*. A small plant arising from a sobole given off by a weak parent usually produces only a few leaves and then sends out a new sobole from which a larger plant is produced next year, and this in its turn may produce a still larger plant before the flowering stage is reached. All the earlier plants of the chain are purely vegetative, and each dies in its turn after producing a larger successor. The successive soboles usually grow out horizontally, but where a plant on a roadside bank has been covered by road-sweepings it sends a sobole vertically upwards which produces a new ring of roots above the old ring.

The first leaves of young plants arising from soboles produced by parents of the *officinalis* and *angustifolia* types are so different from those on the flowering stem that one would hardly think that the young plants belonged to the same species. These first leaves are very similar

in all the forms of *V. officinalis*. Differentiation of the leaves takes place as the plants develop, and in the year before flowering the leaves resemble the lower ones on the flowering stem of the same form.

V. officinalis has a second method of vegetative reproduction, namely, by means of *bulbils*. The bulbils consist of a short pointed bud covered by scale-leaves and emitting one or more roots. This seems to be a new discovery. Irmisch (1853) noted the occurrence of small sessile buds at the base of the flowering stem, and at the base of a daughter plant, but these rooted without becoming detached, and may be regarded as undeveloped soboles producing daughter plants at the very base of the parent flowering stem (see p. 98). On 14 September 1941 my sister-in-law, Mrs. M. G. White, drew my attention to a queer damaged plant of the *officinalis* type near Lower Hilcot (figs. 1–4). On the ground at its base were two bulbils which had fallen off from the lower nodes, and there were five bulbils still attached to the plant. The terminal inflorescence and the uppermost lateral ones were damaged and withered. Two weak flowering branches had arisen from the axils of the node below. A single bulbil in the axil of one of the leaves of the third foliar node from the top had produced three foliage leaves and four roots; the first leaf was unifoliolate and obtusely tridentate at the apex: the second one was trifoliolate, with two small elliptic-oblong lateral leaflets, and a much larger orbicular-elliptic terminal one, cuneate into the base and crenate on the upper margin; the third leaf was still very young, with a pinnately divided lamina borne on its sheath; the two larger roots emerged between the bulbil and the main axis, while the two smaller ones had pierced the sheath of the subtending foliage-leaf of the parent plant. The fourth node from the top bore two bulbils, one in each axil: one bulbil had no roots, consisting merely of a bud, 2 mm. long, which had pierced the sheath of the withered subtending leaf; the other bulbil consisted of a bud and four roots, all of which had pierced the sheath of the subtending leaf; but the bud and the two roots on the left had grown obliquely backwards through the hole in the sheath, while the other two roots had continued growing downwards. At the fifth node there were two very young bulbils, one suberect, 1·5 mm. long, the other very slightly descending, 3 mm. long, and emitting a root (withered in its apical half) 1 cm. long. The sixth node from the top had apparently produced no bulbils. The two bulbils found on the ground had apparently come from the seventh and eighth nodes from the top, each of which exhibited a cicatrix in one of the axils. The crown of the rhizome bore numerous roots and one short sobole.

On the previous day (13 September) I had found by the river Churn, near Colesbourne, a detached bulbil on the ground below a plant of the *sambucifolia* type which had produced two long soboles as well, and had been greatly puzzled by it. On 15 September we found four more plants of the *officinalis-angustifolia* types, near Lower Hilcot, each with a single bulbil at its base. Two of these plants were damaged at the apex. Further search in 1941 was fruitless, but in September 1942 I discovered, near Colesbourne, a miserable specimen of the *sambucifolia* type which was lying flat on the ground beneath cut stems of nettles. It had six bulbils in the lower axils, and five of them had sprouted,

producing one or more small leaves in addition to roots. The sixth had produced only roots. The evidence, as far as it goes, suggests that reproduction by means of bulbils is rare, and is sometimes, if not always, due to unfavourable conditions affecting the parent plant.

Morphologically, there is no essential difference between the bulbils and the sessile buds mentioned by Irmisch as rooting *in situ*. Both arise in the axils of the lower leaves of the flowering stems. The bulbils, however, fall off the parent plant, usually before expanding their first leaves, while Irmisch's sessile buds remain attached to the parent plant until it decays. The soboles differ from both in producing one or more internodes before sending out roots and foliage-leaves.

Reproduction by seed.—The seedlings of *V. officinalis* have been described by Irmisch, who found them in a wild state in Thuringia. These produced from two to five foliage-leaves in their first year, whereas seedlings cultivated by him had ten or more. All the leaves of wild seedlings observed by him had an undivided lamina in the first year, and usually also in the second year, whereas cultivated seedlings produced trifoliolate and pinnate leaves towards the autumn of their first year. The slender primary root dies in the course of the first summer, being replaced by slightly swollen adventitious roots arising from the hypocotyl before the withering of the primary root. Seedlings in their second year, according to Irmisch, are no longer distinguishable from weak plants produced from soboles, as their primary root, hypocotyl, and a short part of the epicotyl have decayed and disappeared. Seedlings in a wild state take several years to reach the flowering stage, but under cultivation they may flower in their second year.

No young plants of *V. officinalis* which could be identified as seedlings have been seen in the Cotswold Hills by the writer. The following facts suggest, however, that the seeds may germinate in copses, in light woodland, and along woodland tracks where the shade is not too dense. In such habitats plants are found in a vegetating condition, but showing no sign of producing a flowering stem, e.g. in a copse near Sapperton, and along tracks in a wood below Shorn Hill and in Chatcombe Wood. Trees were felled in the autumn of 1941 on a sparsely wooded slope near Lower Hilcot, south of the Withington road, and in the following summer many plants of *V. officinalis*, including a considerable range of forms, flowered in the area, although none had been observed flowering on that part of the slope in 1941. Two isolated colonies of *V. officinalis* have been found, one near Little Colesbourne, the other near Pinswell Plantation. In each case all the plants in the colony were so similar as to suggest that they had arisen by vegetative propagation from a single seedling. They resemble a plant from near Lower Hilcot, which Dr. Skalińska finds to be a tetraploid, with 28 chromosomes.

Kreyer's classification.—It now remains to consider Kreyer's work (1930) on *V. officinalis* Linn. He divides it into 17 ' geographical species ', for which he uses binary names. (1) The first dichotomy of his key separates the species with stolons (soboles) from those not possessing them. (2) The next dichotomy in both groups distinguishes species with leaves having long hairs on the lower surface (' folia subtus hirta ') from those

with leaves setulose or glabrous beneath (' folia setacea [*sic*] vel glabra '). (3) Each of the resulting groups is then divided into early-flowering steppe-plants with multipartite cauline leaves (a single species in each case), and late-flowering plants of woods, meadows, mountains, river-sides and marshes. (4) Each of the four late-flowering groups is finally subdivided into two, three or four species, according to the number of pairs of leaflets on the cauline leaves.

(1) The mere absence of stolons—supposing that it is confirmed by cultivation under a variety of conditions—seems a slender character on which to separate species, even if their geographical areas were entirely distinct. *V. Wallrothii* Kreyer seems to differ from *V. angustifolia* Host in nothing but the presence of stolons, and both are recorded by Kreyer from mountain meadows in the ' Schoberstein ' near the town of Steyr in Upper Austria, under the same collector and number (Zimmeter in Fl. Exsicc. Austr.-Hung. n. 3445); he also records both species as collected by Aussersdorfer in 1866 ' in valle Taufers Pustariae '. Furthermore, Kreyer mentions that one of the non-stoloniferous species, *V. palustris* Kreyer, produced two stolons as a result of alluvial flooding (p. 236, fig. 38). According to Todd (1942) a Northumberland population of *V. officinalis* Linn. (*sensu lato*), in addition to producing individuals with no stolons at all, gave a range of stolon length of 2 to 20 cm. The above facts suggest that the absence of stolons on a particular individual is not a very reliable taxonomic character.

(2) *V. repens* Host seems to differ from *V. excelsa* Poir., according to Kreyer, only in the leaves having long hairs on the lower surface instead of being setulose or glabrous. Both are recorded by Kreyer as collected by Stohl in Josefsau Wood near Juvavia, Salzburg: a specimen of *V. repens* is cited by him (p. 194) under Fl. Exsicc. Austr.-Hung. n. 3446 without mention of collector or locality (which are, however, those given above, according to the printed label of n. 3446 in the Kew Herbarium), and one of *V. excelsa* is cited (p. 204) under Fl. Exsicc. Austr.-Hung. without number, but with the same collector's name and locality. Apparently both were distributed under n. 3446. Similarly, according to Kreyer's own description, *V. fenno-scandica* Kreyer and *V. Pleijelii* Kreyer seem to differ in nothing but the indumentum on the lower surface of the leaves. Pleijel (1924) had included both forms under his *V. salina*.

(3) The distinction between steppe-plants and those growing in more humid localities, such as woods, meadows, mountains, river-sides and swamps, does not always hold good. *V. Wallrothii*, which is included by Kreyer (p. 140) in the category of steppe-plants, is nevertheless cited by him (p. 187) as occurring on humid river-banks, in mountain meadows and even in boggy ones, e.g. ' Nied. Öst., Moosbrunn, Sumpfwiese (Witasek et Klammerth) '. *V. nitida* is cited by him (p. 164) from the same locality and habitat: Fl. Exsicc. Austr.-Hung. n. 3444, Austria inferior: ' in pratis uliginosis prope pagum Moosbrunn (Heimerl) '. Comparison of two specimens in the Kew Herbarium, namely, Fl. Exsicc. Austr.-Hung. n. 3444 (mentioned above) and one collected by Gander on the banks of the river Drau at Lienz in south-east Tirol (probably a duplicate of one cited by Kreyer as *V. Wallrothii*), suggests that the only difference between *V. nitida* and *V. Wallrothii* is that the former

has leaves setulose beneath while the latter has long hairs on the lower surface. The two other characters used in the key, namely, the absence or presence of stolons, and the nature of the habitat, have been discussed under (1) and (3).

(4) The number of pairs of leaflets on the cauline leaves seems to afford the best clue to the subdivision of *V. officinalis*. But here again undue weight seems to have been attached to it by Kreyer: the cauline leaves of *V. prorisa* Kreyer are described as having 4–5 pairs of leaflets, and those of *V. palustris* Kreyer as having 6–11 pairs, rarely 4–5 pairs on the lower ones: there appears to be no other difference between the two, and the illustrations of *V. prorisa* f. *dentata* and *V. palustris* f. *dentata* given by Kreyer (p. 239, fig. 3) are remarkably alike. The differences between *V. moravica* Kreyer and *V. repens* Host and those between *V. silesiaca* Kreyer and *V. excelsa* Poir. are equally exiguous, 2–3 (–4) pairs of leaflets compared with 4–5 pairs.

Having attempted to name the European material of *V. officinalis* Linn. (*sensu lato*) in the Kew Herbarium according to Kreyer's revision, I am unable, from herbarium specimens, to demarcate *V. angustifolia* Host, *V. fenno-scandica* Kreyer, *V. Wallrothii* Kreyer and *V. palustris* Kreyer from one another, nor can I separate *V. Pleijelii* Kreyer from *V. nitida* Kreyer. The two latter seem to differ from the four former only in the leaves being setulose or subglabrous on the lower surface instead of bearing long hairs. The six species, taken as a whole, correspond to Drabble's *angustifolia* and *officinalis*.

I am similarly unable from herbarium specimens to demarcate *V. moravica* from *V. repens*, and *V. silesiaca* from *V. excelsa*. The two former have leaves with long hairs on the lower surface of the leaves, the two latter have the leaves setulose or glabrous beneath: the four species, taken as a whole, correspond to Drabble's *sambucifolia*.

Kreyer attached very little weight to the indumentum of the achenes, stating that in the same geographical species these may be glabrous (var. *gymnocarpa* Kreyer), or pilose on one face (var. *secundo-dasycarpa* Kreyer), or on both faces (var. *dasycarpa* Kreyer). But, according to Karsch (1853), the achenes of *V. officinalis* in Westphalia are glabrous, whereas Irmisch (1853) stated that in Thuringia they are usually densely pilose. Two English specimens in the Kew Herbarium (from Shapwick, Somerset, and from Twickenham, Middlesex) have the achenes pilose on one face only (the one-nerved face), while the rest of the British and Irish material seems to have glabrous achenes. These facts suggest that the indumentum of the achenes may serve, in association with other characters, to distinguish varieties.

Summary.

(1) In the Cotswold Hills *V. officinalis* Linn. (*sensu lato*) occurs in the valleys of rivers and streams, and in the smaller dry valleys which run into the larger watered ones. It is found also alongside canals.

(2) The reproduction of *V. officinalis* in the Cotswold Hills seems to be mainly vegetative—by means of *soboles*.

(3) A second and relatively rare method of vegetative reproduction has been discovered—by means of *bulbils*.

(4) Field study suggests that there is only one species of *Valeriana* of the *officinalis* group in the Cotswold Hills, namely, *V. officinalis* Linn. (*sensu lato*).

(5) Judging from study of herbarium material, the same conclusion seems to apply to the British Isles, and to Europe as a whole. Neither Drabble's division of *V. officinalis* into three species, nor Kreyer's division into seventeen species, seems to result in a workable classification. Todd's work (1942) 'points to the great probability that in Britain the forms belonging to the *officinalis* group must be regarded as representng a single polymorphic species'.

(6) About 15 to 20 apparently distinct forms have been observed in the Cotswold Hills. Transplant experiments are required to show how far their characters may be modifiable by change of environment. Breeding experiments are needed to test how far their characters are hereditary: some of the forms may correspond to particular combinations of characters resulting from cross-pollination and perpetuated as clones by means of soboles or bulbils. Finally, cytological examination is required to ascertain the number of chromosomes in each form. According to Kreyer, diploid (somatic number 14), tetraploid and octoploid plants have been found in *V. officinalis* (sensu lato).

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Discussion.—

Dr. Maria Skalińska. I wish to add a few words on cytological investigations made by me on Dr. Sprague's material.

The basic number of chromosomes in *Valeriana* is seven. On the European continent there are diploids (14 chromosomes), tetraploids (28 chromosomes), and octoploids (56 chromosomes). For Great Britain, however, only the octoploid type was reported till now. This number was invariably found by Dr. Barbara Todd; her cytological work is based on plants from 29 localities, well distributed in Great Britain.

In my own studies, however, which are only at the very beginning, I succeeded in establishing the occurrence of the tetraploid type which is represented, along with the octoploids, in the part of Gloucestershire investigated by Dr. Sprague. This presumably older type has evidently a much more limited distribution than the higher polyploid; it is possible that the tetraploids are restricted to some particular habitats, where they seem to occur more frequently than the octoploids.

Detailed studies dealing with the distribution of the two polyploid types within the investigated area in the southern part of Gloucestershire are in progress.

Mr. W. C. Worsdell said that Dr. Sprague's discovery of bulbils appeared to be something new, and asked if it should be regarded as normal.

Mr. Wilmott said that Dr. Sprague's series of specimens afforded a good basis to the opinions of those field botanists who, like himself, had not been able to divide *Valeriana officinalis* into two species by the characters usually given, which certainly were not regularly correlated. Genetical and transplant experiments were desirable. It should, however, be mentioned that Beeby stated that cats in his garden mauled one form and ignored the other, and Drabble had an early paper on the different drug content of the two. He also mentioned that *Dentaria* behaved differently as regards bulbil formation, which was its normal method of reproduction; it produced seeds only under adverse conditions, having been induced to produce seeds in quantity by subjection to harsh treatment, potting in a small pot, bruising and, ultimately, darkness.

Canon F. W. Galpin asked if plants had been raised from the bulbils such as might throw light on the origin of the many varieties which Dr. Sprague had notified.

Dr. Sprague replied to Canon Galpin that he had not been able yet to raise any.

PROCEEDINGS OF THE GENERAL MEETING
25 March 1943

held jointly with The Zoological Society of London

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 11 March 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting:—Dr. A. J. T. Janse, Dr. E. P. Phillips, the Permanent Committee on Geographical Names of the Royal Geographical Society and Dr. E. S. Russell.

Read for the first time certificates of recommendation of the following candidates for Fellowship,—in favour of Benjamin Thornton Cromwell, B.Sc., Ph.D., Julia Hannah Pheasant, B.Sc., and William Percy Jones.

In accordance with Chap. 10, Sect. 8 of the Bye-Laws, the following Fellows were elected, by show of hands, as Auditors of the Treasurer's accounts for 1942–43,—

Representing the Council,—Mr. R. H. Burne and Mr. D. M. Reid.

Representing the Fellows,—Mr. D. J. Scourfield, I.S.O., and Miss E. M. Wakefield.

The proposed Alterations in the Bye-Laws, which had been read from the Chair on 25 February and 11 March 1943, were submitted to a ballot by the Fellows present and confirmed.

The following communication was made and discussed,—

Mr. R. S. Wimpenny. Some aspects of Polarity in the distribution of organisms. (Communicated by the Zoological Secretary. Discussed by the President, Dr. W. T. Calman, Mr. A. C. Gardiner, Dr. R. Melville; Mr. Wimpenny replied.)

Abstract.—

The aspect of polarity discussed refers to an ecological and physiological sequence of organisms between the equator and either pole. It is considered that the gradient of radiant energy between the poles and the tropics sets up a physiological gradient which is readily apparent in a uniform medium such as the sea. This is shown by organisms living more quickly, often accumulating different end-products, occurring in more complex communities, being present in less total mass and numbers, emphasizing the sexual method of reproduction, and showing a bias towards maleness as the tropics are approached.

Plant and animal plankton becomes more abundant in the ocean towards the poles, due, it is suggested, to a gradient of assimilation. This is based partly on the fact that more nutrient salt is brought to the surface by better mixing of the upper and lower water layers, resulting from seasonal variation in temperature in higher latitudes, and partly owing to the increased rate of living towards the equator not being counter-balanced by the means for a corresponding assimilation, more food being needed to support the same mass.

In marine microplankton the quicker living motile and carbohydrate-forming flagellates preponderate towards the equator, the fat-forming diatoms towards the poles. Fat-content in the plankton appears to increase with latitude and for most marine organisms calcification is heavier towards the tropics.

Both on land and in the sea there appear to be more species towards the equator, while in the sea the number of organisms and the whale oil and fish yields increase with latitude. It is concluded that the number and mass of organisms tend to vary inversely with the number of species living in any given habitat; where the habitat conditions remain otherwise the same, a higher temperature and a lower food supply favours specific differentiation and a reduction of the numbers and total mass of organisms.

In many cases among marine animals there is an increase in the size of individuals of a species and among the species of larger groups that runs parallel with increasing latitude. On land, insects of the same genetical stock and mammals and birds are often smaller at higher temperatures. On the other hand, numerous land and marine organisms which suffer seasonal interruption of growth (littoral animals, reptiles, amphibia, bats, etc.) are smaller at higher latitudes.

At lower temperatures and higher latitudes parthenogenesis is more frequent in certain animals. More female than male organisms are

found at lower temperatures and high latitudes in a wide variety of animals and among plants for *Chara crinita* and *Stratiotes aloides*. The same applies to the sex-ratio of a number of human populations. Higher temperatures can turn the sex-ratio towards masculinity by altering the segregation of X and Y chromosomes in *Drosophila* and *Talaeporia*.

The polarity effect is a trend induced by environment, and other external and internal factors may obscure or suppress it.

Discussion.—

The PRESIDENT thanked Mr. Wimpenny and said he admired his courage in covering so vast a field of diverse facts and attempting so bold a generalization. He found Mr. Wimpenny's theory attractive and suggestive, and noted with special interest that it had arisen out of Mr. Wimpenny's fishery research work in this country and in Egypt.

Dr. W. T. CALMAN expressed inability to accept the suggestion that warm and cold blooded animals increase in size for similar reasons. The African elephant is tropical, the Mammoth arctic, and both are large.

Mr. A. C. GARDINER congratulated Dr. Wimpenny on his most interesting and stimulating paper. There were two small points of detail which had occurred to him. In tropical waters, in which concentrations of algae are much smaller than in the polar seas, one finds planktonic blue-green algae, and he asked whether this might not be due to the known power of certain members of the Cyanophyceae to fix gaseous nitrogen. He believed that he was correct in saying that with increased temperature the rate of heart-beat increases, but the length of life of the individual decreases, so that the product of rate of heart-beat multiplied by length of life is approximately constant.

Dr. R. MELVILLE raised the question that it appeared from the data Mr. Wimpenny had placed before the meeting that the various gradients he had demonstrated were centred around 20° S. latitude. He enquired if Mr. Wimpenny could explain why this should be so, rather than that they should be centred around the equator, as might have been expected.

Mr. WIMPENNY replied, in answer to Dr. Calman, that it was admitted that the case of the tropical elephant and the rather smaller pre-historic mammoth was in disagreement with the principle of increase in size with latitude, and it was pointed out that instances of terrestrial mammals obeying this principle were given by Hess from individuals of the same species or nearly related species and not from more widely dispersed groups.

Replying to Mr. A. C. Gardiner, Mr. Wimpenny said that the reason why calcium carbonate was more readily laid down in warmer seas seems to be that, as the dissolved CO_2 was less and the pH index higher than in the colder areas, calcium carbonate would be more easily precipitated.

The following communication was made :—

Dr. A. R. CLAPHAM. The Ecological Society's scheme for a Biological Flora of the British Isles. (Communicated by the Botanical Secretary. Discussed by Mr. I. H. Burkill, Mr. A. J. Wilmott, Miss M. Rathbone, Mr. J. Fisher, Mr. W. T. Stearn, Miss E. Vachell ; Dr. Clapham replied.) [Printed below.]

THE ECOLOGICAL SOCIETY'S SCHEME FOR A BIOLOGICAL FLORA OF THE BRITISH ISLES.

By Dr. A. R. Clapham.

I have been reading, with the object of reviewing them, the first two parts of Dr. Rikli's new book on the vegetation of the Mediterranean lands. The author begins by describing the striking change as one descends the south-facing valleys of the Southern Alps, the change, most marked in spring, from a Central European to a Mediterranean landscape. He proceeds to analyse the flora of the Canton Ticino and finds that 85 per cent. of its species may be regarded as either 'baltic-sylvestral' elements of the central and northern European forest regions, or alpines. Of the remaining 15 per cent., some are thermophilous 'Karst' plants (*Ostrya*, *Celtis*, *Laburnum*, *Fraxinus Ornus*, etc.); some are S. alpine endemics (*Silene Elisabethae*, *Primula calycina*, *Allium insubricum*, *Aquilegia Einseleana*, *Bupleurum speciosissimum*, etc.); some Mediterranean hygrophytes, of shady, usually moist, localities, like *Adiantum Capillus-Veneris*, *Arum italicum*, *Dracunculus*, etc. There remains a small group of 11 species which he terms Mediterranean xerophytes, being five species not native in Ticino, one of which is *Ulex europaeus*, and six indigenous species, *Asphodelus albus*, *Ruscus aculeatus*, *Cistus salvifolius*, *Laurus nobilis*, *Dorycnium herbaceum*, and *Satureia graeca* (? extinct). *Ulex europaeus*, a Mediterranean xerophyte! This was, to me, a new way of regarding *Ulex europaeus*, and I felt I must see what justification there might be for the statement. What, I asked myself, is the European distribution of *Ulex* as a native species? What are its habitats within that area? Where does it grow best? And where is it of most ecological importance? Further, what factors seem to limit its range as a native species? Can it, in fact, grow in dry places in Mediterranean lands, fully exposed to the rigours of the Mediterranean summer? What, in other words, are its preferences and what its range of tolerance, especially in the direction of aridity of substratum and climate?

I was not surprised to find myself unable to answer these questions, and had to resort to the library. Druce's 'Comital Flora' told me that gorse grows in all the vice-counties of the British Isles, though it is doubtfully native in parts of N. Scotland, the Shetlands and the Hebrides. Professor Heslop-Harrison and his co-workers, I found, regard it as almost certainly native in Raasay and Scalpay, and record it for several of both the Inner and the Outer Hebrides. Hegi, in his magnificent 'Illustrated Flora of Central Europe', calls it strongly Atlantic and states that it is probably wild only in the Iberian Peninsula, France, Belgium and Great Britain, though naturalized from S. Scandinavia to Morocco and the Balkans. Rouy and Foucaud ('Flore de France') say it grows in a large part of France, but especially in North, Central and West, being less frequent in South and East and in Corsica. Briquet says it is absent from the south of Corsica. Fiori and Paoletti record it from northern Italy and here and there further south.

With regard to habitat, Professor Fritsch and co-workers found it frequent only in the valleys on Hindhead Common; Tansley and Adam-

son, and Watt describe it as much more characteristic of the non-calcareous loams of the South Down chalk heaths than of the calcareous chalk grassland, but do not regard it as a calcifuge. E. W. Jones records it as often following disturbance or burning, but in some cases colonizing *moist* sites. There is much scattered information about its resistance to fires, and about its susceptibility to frosts, even in Devon and in Ireland. Professor Weiss showed how ants play an important part in dispersing it along paths. On the Continent it is especially characteristic of NW. Spain and north Portugal, where, pure or mixed with other shrubs, it covers enormous areas of hillside on all kinds of soil, as well as forming a shrub layer under oaks and pines. This, undoubtedly, is its true home. It falls off rapidly in abundance from north to south Portugal, but is still prominent. In France it is described as chiefly on siliceous, rarely on calcareous soils ; in Corsica as calcifuge, and a constituent of garigues of the lower zones ; and in Italy as in sterile places of the Mediterranean and sub-montane zones. Rikli himself describes it as forming the shrub layer under *Pinus pinea* near Pisa and Ravenna. In Germany it is extensively naturalized following planting for deer, cattle and horse fodder ; but is everywhere severely injured by hard frost, often being cut back to ground-level.

The point I wish to make by recounting this story of a piece of bibliographical research is that there is already a great deal of published information about *Ulex* of the kind I was seeking—information which is, however, not readily accessible. There are gaps, to be sure ; what, for instance, happened to gorse in this country during the hot, dry summer of 1921 ? Where exactly does gorse grow in Corsica and southern Italy ? and many more such questions could be posed ; but most might be answered if there were a means of drawing on the knowledge and experience of local botanists and naturalists.

It is not only academic botanists who want this autecological information about individual species. It is often vital to biologists of many kinds to know details of the distribution, abundance, life-history, tolerance and intolerances of species of economic importance, or of significance as indicators of climate and soil, or as hosts of economically important insects or fungi. It is well known that many inquiries of this kind have already been made since the war began. It is clear also that such knowledge, in convenient form, will be of great value to the ecologists, taxonomists, pathologists, foresters, agriculturists of the future.

Already in 1870 Hooker suggested that it would be useful to have a companion volume to his ' Student's British Flora ', a volume in which ' physiological and morphological observations ' on British species might be recorded. Since that time there have been several works published on the Continent whose object has been much what was in Hooker's mind :—Raunkiaer, Kirchner, Loew and Schröter, Schröter's ' Pflanzenleben der Alpen ', and even Hegi's great Flora. None, however, is British, and they have had either a narrower scope than Hooker envisaged, or have never been completed.

In 1928 the British Ecological Society decided to make a move in this direction, and Professor Salisbury, in a note on the Proposed Biological Flora of Britain, invited the active co-operation of both professional

and amateur botanists. 'Much relevant information', he wrote, 'is to be found scattered through the multitude of botanical journals, but is difficult to access. A great deal is also known to field naturalists, but has never been published, and is likely to be lost with the death of the individuals. It is proposed to incorporate in the Flora all accessible published observations, together with the not inconsiderable mass of unpublished data. It is felt that such a compilation will be of great scientific value, and at the same time provide the surest means of bringing to the notice of students the many lacunae that require to be filled'.

In January 1940, the British Ecological Society decided that the time had come to begin publication of the new Flora. The policy adopted was to invite members of the Society or others interested to offer to compile accounts of individual species or groups of closely-related species. A small Editorial Committee was instructed to draw up, for submission to the Council of the Society, a Schedule for Contributors, and to prepare the first accounts. The Schedule was intended to show the proposed scope of the accounts and to provide a plan for them; not a plan to be followed slavishly, but one which would impose some measure of uniformity of treatment. In the accompanying Foreword the primary aim of *compilation* and the vital necessity of *co-operation* were re-emphasized. The accounts were to be summaries of information at present available about each species, rather than miniature monographs. They were not to be published in any regular order, but species would be dealt with as the necessary information became available, and by contributors with a special knowledge of or interest in particular species. Additions and corrections would be published when necessary. One of our difficulties has been the somewhat formidable appearance of the Schedule, but it has seemed important always to keep in mind the whole body of information which it would be ideally desirable to find in our Flora, while continuing to stress the importance of merely collecting what is already available.

Accounts already published are those of the genus *Juncus* and four species of *Juncus*; the genus *Zostera* and two species; *Cladium Mariscus* and *Aster tripolium*. Five or six are in the hands of the Editorial Committee, and nearly a hundred others have been promised.

The Committee have been fortunate in the assistance of Professor O. W. Richards and Dr. A. Smith, the former having undertaken to edit lists of insects and Dr. Smith the lists of fungi which merit special mention in connection with individual species of flowering plants.

Many pressing problems have been forced on the attention of the Committee. One specially troublesome set of problems are those of taxonomy and nomenclature. We have no modern British Flora to follow in these matters, and it has been necessary to give some lead to contributors so as to avoid chaos. A statement has been prepared which instructs contributors to follow the International Rules of Botanical Nomenclature, and if in difficulty to consult the Editorial Committee and its advisory taxonomists. It was decided, however, that all specific epithets, whether of plant or animal species, should be printed with small initial letters. With regard to the much more difficult problems of taxonomy, an attempt has been made to secure uniformity in the use of

accepted taxonomic terms, and to incorporate the findings of cyto-genetical research into current taxonomic practice.

Other difficulties have arisen as a result of the war—the increasing restrictions on travel, and the more pressing claims of other forms of activity. But it is hoped that the work on the Flora will go forward steadily if slowly until the clouds lift. Meanwhile, on behalf of the British Ecological Society I should like to invite your criticism, your advice and your co-operation.

Discussion.—

Mr. I. H. Burkill said that as the Botanical Secretary he had greatly welcomed the suggestion made to him by Professor F. T. Brooks that the Ecological Society's scheme for a Biological Flora of the British Isles should be discussed at a meeting of the Linnean Society, and how gratified he was when Dr. A. R. Clapham consented to explain the scheme. He added that he considered the Flora to be a great desideratum and so fully approved of the scheme as to work for it: he added that he spoke with the experience of having written up *Tamus communis* for it. His difficulties in fitting an account of this plant to the scheme had been in compression, but as *Tamus* is aberrant his would not necessarily be those of other workers. He had found it difficult to compress into a reasonable amount of text all that the scheme provided for concerning associated plants and soils towards which it is tolerant. He begged for an interest in the scheme and aid in forwarding it.

Mr. Wilmott said that although he had previously discussed this subject with Dr. Clapham there was one point he wished to emphasize, viz., that there was much information which was not being collected. In connection with a draft on *Aster Tripolium* he had collected a large number of references by consulting a few years of Just's 'Jahresbericht', which should be consulted as a matter of routine. There was also much personal unpublished information which was not obtained, e.g., the distribution maps given for *Juncus effusus* and *J. conglomeratus* treated the Outer Hebrides similarly, but in fact he knew that *J. conglomeratus* was there ubiquitous and abundant whereas *J. effusus* was almost non-existent. He suggested the possibility of printing a draft and circulating it to persons who were likely to have information or be able to collect it, and (after leaving a whole working season for confirming impressions if necessary) publishing the final form after collation of the further information received.

Mr. W. T. Stearn. As one primarily interested in Systematics and plant-geography I should like to say a little about the portrayal of geographical distribution in the Ecological Flora. This can be done by shading entirely the vice-counties from which the species is recorded or by marking with dots the individual localities. The maps in the published accounts I have seen employ the shading method, but for species with a narrow range of tolerance and a restricted distribution this can be rather misleading. Thus, for *Narthecium ossifragum* and other 'Atlantic' species, the dot map gives quite a different impression from the map with the whole vice-counties shaded, and naturally it brings out much more accurately the areas in which the species is rare

or lacking. This is important when, as with *Narthecium ossifragum*, the species has special requirements and in certain vice-counties occurs only near the vice-county boundary. The shaded vice-county map makes the range of such species appear more extensive than it really is, and may obscure interesting features.

Miss E. VACHELL asked: (*a*) whether the amount of scent emitted varies in different localities; (*b*) whether it is on the increase in some species and on the decrease in others; (*c*) whether the scent increases when the plant ceases to lose colour as an allurement to insects, i.e., *Aster Tripolium* var. *discoideus* Reichb. which is now much more abundant in some districts than the type and emits a strong honey-scent.

PROCEEDINGS OF THE GENERAL MEETING
8 April 1943

held jointly with the Zoological Society of London.

Dr. E. S. RUSSELL, O.B.E., M.A., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 25 March 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting:—Mr. J. B. Scrivenor, John Innes Horticultural Institution and Svenska Linné-Sallskapet.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted,—Dr. John Smart.

The President reported the death of Sir Edwin J. Butler, C.M.G., C.I.E., F.R.S., Fellow of the Society.

Read for the second time certificates of recommendation of the following candidates for Fellowship: in favour of Benjamin Thornton Cromwell, B.Sc., Ph.D., Julia Hannah Pheasant, B.Sc., and William Percy Jones.

Read for the first time certificates of recommendation of the following candidates for Foreign Membership:—Professor Carl Johan Fredrik Skottsberg and Dr. Alfredo Ramalho.

Read for the first time certificates of recommendation of the following candidates for Associateship, *honoris causa*:—Thomas William Burton and Charles Biddolph.

The following communication was read and discussed:—

Sir THOMAS HOLLAND, K.C.S.I., K.C.I.E., F.R.S. 'The theory of Continental Drift'. (Discussed by the President, who communicated the paper, Lt.-Col. R. B. Seymour Sewell, Dr. A. T. Hopwood, Prof. A. C. Hardy, Dr. F. E. Zeuner, Prof. G. D. Hale Carpenter, Dr. G. P. Bidder and Mr. K. N. Kaul; Sir Thomas Holland replied.) [Printed below.]

THE THEORY OF CONTINENTAL DRIFT.

By Sir Thomas H. Holland, K.C.S.I., K.C.I.E., F.R.S.

Recent controversies about the theory of continental drift seem, at first glance, to show that the evidences for and against the theory are at the present time wholly irreconcilable.

Followers of the late Alfred Wegener assert that the geological record cannot possibly be explained except on the assumption that, since about the middle of the Mesozoic era, the great continents became separated by horizontal sliding to distances up to as much as 3000 to 4000 miles, which, for example, now separate the New World of the Americas from the Old World of Eurafrica.

Geophysicists, on the other hand, state quite definitely, and with obvious unanimity, that movements on this scale are mechanically impossible. Following the suggestion made by Richard Oldham (1900) over 40 years ago, seismologists have shown that the earth is effectively solid and of a strength comparable with that of surface rocks down to about half of its radius : that fractures following local differential stresses generate earthquake waves from points as far down at least as about 600 miles from the surface. There is no disputing this plain statement of reasonable fact.

My own intervention in this controversy is merely to point out that what the seismologists find to be true today does not necessarily, or even probably, apply to the state of the earth's outer shells towards the end of the Mesozoic times, some 70 million years or more ago, when activities of the order of a revolution occurred, followed by uprise of the great Tertiary mountain ranges.

So that is the situation which we have to discuss, and my contribution to the discussion will be limited to the first and third sections, namely, (1) that there is evidence to show that drift on a large scale almost certainly started just before the Tertiary period was inaugurated ; and (2) that the geological record shows a large-scale activity to have occurred among the outermost shells of the earth round about that time.

Evidence in support of the theory.—The evidence in favour of the assumption that large-scale horizontal continental drifts have occurred falls into two classes : (1) geological records of a kind which, so far as anyone can see, cannot otherwise be explained except by long-distance drifting ; and (2) a much larger body of facts which would readily be understandable and quite simply explained if what seems to be a plausible hypothesis could first be promoted to the higher caste of theory. The first group of facts are, according to present knowledge, crucial. The second group will naturally lose their scientific value as accessory support, if the crucial evidence fails to stand up against cross-examination.

In view of the suggestion that it was in Mesozoic and early Tertiary times when geophysical conditions permitted the assumed drift, some of the arguments recently used to support the theory may be put aside as irrelevant. For example, recent apparent changes of longitude. These are regarded reasonably by geodesists as due possibly only to comparing old observations with the more accurate determinations made during

the past 50 to 70 years. And such modern changes of longitude, even if proved, cannot be quoted in support of the assumption that continental drift occurred as long ago as in Cretaceous times. In any event, their evidence is not really wanted to show the possibility of horizontal movements of the crust. The folding of mountain ranges during Tertiary times—ranges like the West American Cordilleras, the Atlas, Alps and Himalayas—show horizontal movements variously estimated to reach hundreds of miles. These movements, forcible enough to fold large masses of strata over one another, are admitted on both sides. They are regarded by Dr. H. H. Jeffreys as the result of the collapse of the crust on a cooling and shrinking earth. He revives the old popular idea in a more rational form, based on a mathematical analysis of physical conditions, which we need not discuss now, because movements of the sort are wholly different in kind and dimensions from transoceanic journeys of thousands of miles such as are pictured by those who support the hypothesis of continental drift.

Biological distribution.—The present difficulties of accounting for the distribution of animals and plants would be simplified if we were allowed to move the continents about as freely as icebergs are driven by oceanic currents, and the satisfactory solution of this problem might be regarded as among the dependent accessory evidences. Professor Schuchert (1932) of Yale, in an elaborate memoir reviewing the evidence of palaeozoology down to the Silurian, found it necessary to assume that 'land bridges existed during Palaeozoic and Mesozoic times in the Atlantic between Brazil and Africa and between Africa and India'. And Schuchert has declared himself to be an agnostic regarding the new revolutionary gospel of continental drift, although he found himself driven on this occasion to trim down Dana's original and comprehensive declaration that 'the continents have always been continents . . . . and have never changed places with the oceans'.

In his Presidential Address to the Geological Society in 1890, W. T. Blanford (1890), reviewing the Upper Palaeozoic and Mesozoic biology of India and the southern continents, formally broke away from Dana's doctrine of permanence which had hampered Huxley when he addressed the same Society twenty years earlier, and had embarrassed Charles Darwin when he wrote chapters XII and XIII of the 'Origin of Species'.

Blanford had to postulate a hypothetical continent of gigantic size stretching over the area now occupied by the Indian and South Atlantic basins and including India, Australia and South America, to which later workers added Antarctica—the supposed continent which Suess named Gondwanaland. Those of Blanford's arguments, which were based on the distribution of the *Glossopteris* flora, were endorsed in 1907 by David White (1907), the American palaeobotanist, in these words:

'The occurrence of this flora in great uniformity, including an extraordinarily high degree of specific identity, and in relative purity, contemporaneously in India, Australia, South Africa, and southern South America, leaves no recourse but to conclude that the land surfaces over which it extends (Gondwana) were in such continuity, or intimate

geographical relation, as freely to permit the migration of the flora, practically *in toto*, between all these quarters of the globe '.

Presumably, I need not mention in this room the pitfalls which may trip up those who rely on the facts of biological distribution. The geological record is far too incomplete to rely on negative evidence, especially when dealing with the origin of land animals, such as the marsupials and struthious birds which are characteristic of the southern continents. No one, however, has so far questioned the conclusion that the southern spread of the *Glossopteris* flora over continents as widely separated as Australia, Africa, South America and India required a former land communication of *some* sort ; still, very recent work by Sahni and his active band of disciples in India makes one think twice even about this question ; for they have been finding in India and Australia several kinds of winged spores in otherwise barren shales in the Lower Gondwana beds ; and, naturally, one wonders whether such spores might not have been distributed by winds or ocean currents from one continent to another. This reminds one of how Darwin collected much evidence and made many experiments to show that plant seeds and many small animals obtained the benefit of occasional, accidental and quite unexpected means of transport across the seas ; but he confessed that he could not provide suitable rafts for the large dry-land animals. Nor did Blanford rely only on the wide distribution of the *Glossopteris* flora. In addition to his quotation of other evidence from freshwater invertebrates, he analysed what was then known of the striking relationships between the Permian and Triassic reptilian remains on some widely separated fragments of his supposed Gondwana continent.

Fellows of both Societies present will recall other examples of distribution which would be easier, even quite easy, to explain if one were allowed to postulate either one of two alternative forms of past overland communications : either (1) the former existence of continental stretches across areas now occupied by deep and wide oceans ; or (2) a subsequent drifting apart of continental fragments which were once sufficiently near enough to one another to permit of free migration.

Either of these alternatives seems to be as good as the other from the biological point of view. Blanford in 1890 never thought of continental drift ; so he attacked J. D. Dana's doctrine (1881) of the permanence of continents and oceans, which at the time was accepted by every leading biologist except Edward Forbes (1846).

At present, so far as one can understand the facts of biological distribution, therefore, they are not inconsistent with the theory of continental drift, but still that theory must be based on other and quite independent evidence.

It is proposed, therefore, to call attention to some evidence which, so far as one can judge, can be interpreted in no other way than by assuming that continental drift actually did occur. This evidence is quite inconsistent, both with Dana's doctrine of permanence and with Blanford's alternative theory of the foundering of ancient continents to produce modern deep oceanic basins. The theory of continental drift demands, according to geophysicists, a mechanical impossibility ; whilst Blanford's idea of sinking continents equally conflicts with the principles

of isostasy. And isostasy was, of course, active in Mesozoic times, as it is today. The conditions favouring drift, however, may have been quite different then.

Southern Carboniferous glaciation.—The evidences in favour of drift, which may be regarded above all as definitely crucial, are contained in the records of widespread glaciation in Upper Carboniferous strata which were recognized in India in 1857, and long afterwards in four of the Australian States, in South and Central Africa, in Madagascar, the Falklands, in the Argentine, Uruguay and the present tropical parts of Brazil.

It is important to understand distinctly that these glacial deposits are not ordinary mountain-valley moraines; they cover many square miles, often—indeed generally—flat-bedded and interleaved with fine shales, sometimes obviously of freshwater origin, sometimes marine. They are not to be explained away as the results of elevation or local special meteorological conditions.

They are known only at one horizon in India and one in South Africa, but they occur at four other horizons in the Carboniferous of Australia and two others in the Argentine. In my first Presidential Address to the Geological Society (1933), I gave details sufficient to show that one of the beds in Australia was almost certainly contemporaneous with that in India, and nearly, if not exactly, contemporaneous with that in South Africa, as well as with the uppermost of the three in South America.

Here, then, we have glacial conditions occurring at the same time, ranging over tropical India and up to 30° North latitude, as well as from within the present tropics to similar latitudes south of the equator in all the other continents. This distribution of glacial conditions has been a baffling mystery for more than half a century, and all sorts of explanations have been vainly offered, each in turn breaking down on the slightest examination, before anyone thought of the possibility of large land fragments floating off from an original continent in the Antarctic region, taking with them their basement formations, on which rest the Upper Palaeozoic boulder beds, with their accompanying coal-measures, as well as overlying formations up to near the top of the Mesozoic column.

All-world refrigerations have doubtless occurred at various times in the past, as they did in the so-called Great Ice Age of the Pleistocene period; but, as Sir George Simpson (1930) has stated with recognized authority, so long as the earth has been rotating on its present axis inclined to the ecliptic, the climates must always have been zoned from a warm or relatively mild equatorial belt outward in both directions to the higher latitudes, both north and south. If, then, glacial conditions actually prevailed at any time at sea-level over the tropical belt, the whole world would have been encased in ice; and that we know to be untrue for all past palaeontological time. We could hardly think of glaciation at sea-level in the tropics, and corals flourishing in our own seas at the same time. Anyone who can find a flaw in this form of reasoning from the abundant and consistent evidence will shake my faith in the drift theory. But if the conclusion on this one point be

admitted, we can search more hopefully for physiographical conditions which will satisfy the geophysicists.

Special characteristics of the older basement formations.—That being regarded as the most important of crucial tests, we can now call in some of the other witnesses referred to as giving accessory forms of evidence which can be most easily interpreted by the drift theory, but which possibly might still be found to admit of other explanations. If, as we now assume, some old southern continent, previously situated within or near the Antarctic region up to at least about the end of Palaeozoic times, broke up, those of its fragments which moved to better climates or drifted westward would be expected to show other peculiar characteristics in common, both older and younger than the Upper Palaeozoic coal-measures and associated glacial formations. The basement rocks below the glacial formations should also include peculiarities common to two or more of the scattered fragments of the original continent. And, indeed, they most certainly do so. For example, the charnockite series—a most peculiar group—first found fifty years ago among the fundamental crystalline rocks in South India, have since been discovered in Central Africa, Madagascar and Antarctica. They have not so far been reported in the other continents ; but their discovery in northern regions would merely show that, like granites and basalts, they are not peculiar or distinctive to the basement of the southern continents ; in other words, they would not be of much help as accessory witnesses, but would still not be inconsistent with the drift theory.

More satisfying and safer support is, however, obtainable from the occurrence of glaciations much older than the one which is now so well known in all the scattered parts of the supposed old southern continent, and these have now been found in the Lower Palaeozoic as well as in pre-Cambrian groups in both South Africa and Australia, as well as the Falklands, at latitudes which are now some 65° to 70° from the South Pole ; and as it is not likely that any Antarctic ice-cap ever extended so far north, these occurrences suggest that South Africa and Australia at least were both previously nearer the South Pole than they are now. The absence of reports of similar very ancient glaciations from other parts of the supposed old Gondwanaland, India and South America, may mean that the primitive continent was not all of it exposed in those times to antaractic rigours, or, more likely, may mean that the other fragments have not yet been sufficiently explored.

There are some other forms of accessory evidence which suggest even more strongly that continents which are now widely separated were once nearer, even quite near, one another. For example, the remarkable agreement in the geological features of West Africa and the eastern parts of South America.

Geological correspondence between Africa and South America.—A map which Du Toit (1927) published in 1927, following a special visit to South America, compares the opposite shores of the South Atlantic from Patagonia to the Guianas on one side with Africa from the Cape to Sierra Leone on the other, showing how closely the formations correspond in

their peculiarities, stage by stage, up to the marginal marine transgression at the end of the Mesozoic era, and showing, too, a significantly remarkable agreement in the order of succession, as well as the detailed matching of the subdivisions, lithologically and palaeontologically. This extraordinary correspondence between the two areas impresses everyone who has seen parts of both areas, although no single person has gone over all the ground on both sides of the Atlantic. The only parts of the world in which the peculiar diamond-bearing pipes occur are in these two areas significantly.

Then again, the parallel tectonic lines on both sides of the ocean suggest fold movements which probably affected a single continental mass originally; for they could hardly have occurred independently on lands so widely separated from one another as they are now.

In Cape Colony there is a thin band of black clay in the Dwyka series; and at the same horizon in South America the Iraté shale is composed of exactly similar material, also forming a thin bed. In each area there are well-preserved remains of a small, primitive, free-swimming reptile, *Mesosaurus*—obviously a delta scavenger—which is not known elsewhere in the world. If South Africa and South America were always separated, as they now are, by an ocean 4,000 miles wide, it is very unlikely that the bones of *Mesosaurus* would have been found in both areas, and in similar deltaic clays very nearly, if not exactly, of the same age. If, however, these two continents were at one time close to one another, *Mesosaurus* would naturally have found it possible to get round from one river delta to another nearby. What we can say justifiably at present with regard to the evidence of *Mesosaurus* is that his occurrence can reasonably be regarded to support the idea that South America and South Africa were at one time much nearer to another than they are now, near enough to permit of the migration of an animal that certainly could not travel overland and almost certainly would not have attempted an ocean journey.

Contrast of Glossopteris and Gigantopteris floras.—In recent years there has been a considerable increase of our knowledge of the fossil plants preserved in the Permo-Carboniferous and later formations in Western China, Indo-China, and Sumatra, and these new data again quite unexpectedly form another important piece of circumstantial evidence which fits in with the idea that this part of the Asiatic region, in later Palaeozoic times at least, was separated from Gondwanaland by a barrier which could not be crossed easily, if at all, by migrating plants.

The assemblage of Palaeozoic fossil plants of this Indo-China region, generally known as the *Gigantopteris* flora, has quite recently been critically examined by T. G. Halle, B. Sahni and others, who show that, contrary to previous impressions, the *Gigantopteris* flora contains no species in common with the widespread *Glossopteris* flora of Gondwanaland. The plants which lived in the region where *Gigantopteris* flourished indicate the existence then of a warm, moist climate with luxuriant vegetation, whilst the *Glossopteris* flora lived in a comparatively cold climate. According to Sahni (1938), 'we know of no other two floras,

living or extinct, which are floristically and climatically so distinct ; and yet they now lie side by side on the map ; crossing the same latitudes along a north-south front of well-nigh two thousand miles '.

This evidence from the fossil plants, found unexpectedly only three or four years ago, is in striking agreement with the assumption that the part of Gondwanaland which is now contiguous with the Indo-China region was widely separated from it in late Palaeozoic times.

These selected samples of evidence seem to require, so far as our present knowledge goes, continental drift on a large scale for their explanation. They also seem to be quite independent of one another ; the failure of any one of them to stand cross-examination would not apparently invalidate any other. There are, of course, many other forms of evidence that might be called, and there is a still larger number of observations which could be explained satisfactorily if it were legitimate to admit that drift was physically possible on an earth constructed as it may have been in Mesozoic and early Tertiary times. Even, however, if no single piece of accessory evidence now quoted could be regarded as crucial, when considered alone, the ' cloud of witnesses ' telling a similar story is surely too significant to be put aside lightly.

Possible reconciliation of the geophysical and geological evidence.—The geophysicists say definitely, and cannot be contradicted, that the earth is effectively rigid down to hundreds—probably to some 2000—of miles, where the solid ultra-basic silicate rocks pass into the core of molten nickel-iron, which does not transmit the transverse, torsional earthquake waves. On the other hand, some geologists say that the plain facts cannot be explained without a wide scattering of continents which were, up to Mesozoic times, near one another.

The supporters of the drift theory refer only to movements of the superficial skin, possibly 10 or 15 miles thick ; and this only partly covers the basic shell, which may be 20 to 25 miles thick, forming a complete envelope. The granitoid ' cakes ' which form the continents are regarded as floating in isostatic equilibrium on the basic shell, and are insufficient in area to cover the whole earth. For example, on the bottoms of the deep oceans, like the Pacific, the basic shell is probably exposed. These ideas seem to be common to all parties and are fairly well established.

It is known, too, that the radio-active elements are mainly concentrate in the outermost rocks, and the heat produced by atomic degeneration accumulates under the continental blankets, sufficient, possibly, to produce fusion of the uppermost layers of the basic shell. This was the foundation of the theory proposed by Joly (1923) twenty years ago. Joly estimated that every 40 or 50 million years widespread fusion of the sort occurred, with tidal movements and the out-welling of basic magmas, followed by refrigeration and then another period of rest for the accumulation of heat.

During the molten phase there would be a reduction in the density of the basic magma and a consequent sinking of the continental blocks, with, therefore, trespass of the ocean over part of the land. Such trespasses in the past are known ; they were recurrent but not apparently

periodic. One of them occurred towards the end of the Mesozoic era ; that is, near the time when continental drift was apparently active. It was near that time also that there occurred widespread outflows of basic lava ; and these almost certainly were but surface signs of a much wider area of melting below.

And then in the Tertiary period, following these signs of widespread melting of the basic shell, there arose our great mountain ranges—the Alps, the Caucasus, the Himalayas, the Atlas, and the still longer stretch of Cordilleras along the western margin of the Americas, North and South.

There is thus evidence to show that some 50 to 70 million years ago there was a widespread physical revolution of a kind which might have facilitated continental drifting. Facilitated, may be ; but we still have to find evidence of a sufficient motive force to cause the horizontal thrusts. In any event, the whole question deserves further consideration from the geophysical point of view ; for this aspect of the problem seems to have been overlooked by those who state, without qualification, that continental drift is a mechanical impossibility.

There I must leave the subject with a repetition of the remark for consumption by geophysicists : they are obviously right in what they say of the earth's crust today, but not necessarily right, or even probably right, in applying the seismological records of today to conditions which prevailed in early Tertiary times, when, according to geological evidence, continental drift seems to have occurred.

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Discussion.—

The President said that he had greatly enjoyed the address by Sir Thomas Holland ; but, not being an expert, he proposed to leave the discussion of it to others more competent than himself, and he called on Lieut.-Col. R. B. Seymour Sewell to make a contribution which he had promised.

Lieut.-Col. R. B. Seymour Sewell. According to the Wegener Drift Theory the Pacific and Antarctic Oceans were the only original marine areas, and the Indian, Atlantic and Arctic Oceans were formed at a later date. A study of the floor of the oceans suggests that these attained their present condition in the Tertiary Epoch. Such rock samples as have been dredged from the bottom of the oceans are basalt, and the age of one specimen, obtained by the Percy Sladen Expedition to the Indian Ocean, which was examined by Dr. Wiseman, was found to consist of a mass of basalt fragments welded together by calcite, in which was embedded a foraminiferan which could be dated, and which was Tertiary. All oceanic islands, with the exception of the Seychelles in the Indian Ocean and St. Paul's Rocks in the Atlantic, are volcanic or composed of coral, and where it has been possible to assess their age this too is Tertiary. In each ocean there is a great sub-marine ridge, and in the Indian and Atlantic Oceans this separates these oceans into eastern and western troughs: at their southern end these ridges tend to bulge eastward. A similiar bulge to the east is seen in the Scotia Arc, joining South America and Antarctica. In each case this bulge lies between Lat. 50°-60° S. If, as Wegener suggests, the continents drifted westward, the underlying semi-fluid basalt magma must have flowed eastward, either underneath the continents and welling up behind them, where a ridge would thus be formed, or between the southern ends of the continents and Antarctica, in which case a series of waves would have been developed. It would be extremely interesting to hear from an expert in hydrodynamics what waves might be expected to develop in these circumstances and how far the present sea-floor corresponds to such waves.

Most of the zoological evidence that has been adduced in favour of the drift theory has been drawn from land organisms, but we should be able to get evidence from a study of marine organisms also. I have analysed the composition of the warm-water epiplanktonic Copepoda of the different oceans; and I would point out that their present-day distribution appears to have been brought about in the main by the existing surface currents. The results of this analysis are extremely interesting. In the late Carboniferous era the originally single continent of 'Pangaea' began, according to the drift theory, to fragment by the formation of a series of rifts; at their inception these must have resembled the Rift Valley of Africa, and have been filled with fresh water. At the commencement of the Tertiary epoch narrow gulfs had formed between America and Africa and between Africa and India, and from the southern ends of these gulfs a connecting narrow sea ran eastward to the Pacific, being bounded on the southern side by the combined mass of Antarctica and Australia. In these two narrow gulfs the conditions probably very much resembled those of the Baltic Sea of today, for, owing to the large number of great rivers that flowed into them, the surface water must have been brackish.

The immigrating fauna, however, must have been swept in from the Pacific Ocean and equally must have been marine. Such an immigration must have been accompanied either by adaptation of marine species to brackish-water conditions or by the evolution of new species that were

adapted to brackish water but were derived from marine ancestors. Finally, with the complete separation of the continents, we should get the present-day condition, namely, a large marine area, with small brackish-water regions off the mouths of each of the great rivers.

In the accompanying table I have given the numbers of the surface-living warm-water epiplanktonic Copepoda in the different oceans; and, since the general trend of their distribution seems clearly to have been from east to west, I have assumed that the most easterly record of the distribution of each species indicates its place of origin. In the

Region.	Total number of species.	Number of indigenous species.	Number of endemic species.	Number of species in fresh or brackish water.	Number that have reached				
					W. Pacific.	Indian Ocean.	Red Sea.	Suez Canal.	Atlantic.
E. Pacific	141	133	10	5	113	111	70	12	100
W. Pacific	243	122	35	19	..	77	24	8	34
Indian	274	78	48	38	..	..	5	2	20
Atlantic	259	105	91	58	..	8	..	..	..

first column we have the total number of species so far recorded from each area. This number steadily increases as we pass westward from the East Pacific to the Indian Ocean, and then falls slightly as we enter the Atlantic; this fall is undoubtedly due to the difficulty experienced by some species in getting round the southern end of Africa, where there is a mixture of ocean currents that causes a marked fall in temperature.

In the second column I have given the number of 'indigenous' species, i.e., those that appear to have originated in each area, and here we find a steady fall from east to west, the greatest number having originated apparently in the East Pacific region, fewer in the West Pacific, fewer still in the Atlantic, and least of all in the Indian Ocean: but it must be remembered that the area of the Indian Ocean is considerably less than either the Pacific or the Atlantic Oceans, for there is no North Indian Ocean.

In the series of columns on the right of the table I have given the distribution of these species. Of the indigenous East Pacific fauna the great majority of species are cosmopolitan; this may be due, in part, to the old connection that existed in early Tertiary times between the Atlantic and Pacific Oceans, across Central America: but, on the other hand, it may be that this East Pacific fauna has had time in which to spread westward through all the great oceans.

Of the East Pacific fauna 75 per cent has reached the Atlantic and 54 per cent the Red Sea. Of the West Pacific fauna 47 per cent has

reached the Atlantic and 20 per cent the Red Sea ; while of the Indian fauna 26 per cent has reached the Atlantic and only 6 per cent the Red Sea. Of the Atlantic fauna eight species have succeeded in getting eastward into the Indian Ocean, but these appear to have been carried there by the deep current of the North Atlantic intermediate water. Clearly, then, if the area occupied by a fauna is an index of its age, the East Pacific is the oldest and the West Pacific and Indian faunas are more recent. In the older ocean there has been time for the evolution of the larger number of new species.

Turning now to the number of species that appear to be ' endemic ', i.e., those that are restricted to any one ocean or part of one ocean, the fewest are found in the East Pacific area and the greatest number in the Atlantic. If we agree with Willis that an endemic species is, or may be, a young one that has not yet had time in which to spread to additional areas, then once again it seems to be indicated that the East Pacific fauna is the oldest and the Atlantic fauna the youngest.

In the last column to be considered I have given the number of species belonging to marine genera that have been able to penetrate into brackish or fresh water and establish themselves in these new surroundings, sometimes with the production of a special local race. Some of the species that have been able to populate these areas are of world-wide distribution, while others are extremely localized in their habitat and are known from an isolated locality, such as the mouth of a particular river, or from a small area along a particular coast. Many of these latter belong to the family Centropagidae (sensu lato), which includes, among others, the marine genera *Centropages*, *Pseudodiaptomus* and *Eurytemora*. Brehm and Zederbauer (1902), Steuer (1910) and Tollinger (1911) have all reached the conclusion that the world-wide distribution of this family began about the middle of the Tertiary epoch and has continued through the Quaternary into post-Glacial times. All three genera, and especially the last two, provide numerous instances of species that have invaded brackish or even fresh water, and it seems probable that in the middle of the Tertiary epoch, when the newly formed Indian and Atlantic Oceans were largely filled, especially as regards the surface-layer, with brackish water, ancestral marine species were carried into these oceans and became adapted to the brackish conditions ; but, as the oceans gradually widened, brackish-water areas slowly became cut off from each other by true marine regions, and thus, possibly as a result of isolation, new species were evolved, so that we now find distinct species inhabiting the mouths of nearly all the great rivers. So recently did this occur that in many instances the species is confined to a single river, though some have been able to spread for a short distance along the coast, while others have penetrated up the river into fresh water. We thus get distinct sets of species inhabiting the Ganges and Brahmaputra estuaries in the Bay of Bengal and Quilimana River in East Africa, all in the Indian Ocean, and others in the Congo and Niger Rivers of West Africa, and the Amazon, Mississippi and St. Lawrence Rivers of America in the Atlantic Ocean.

It would thus appear that the drift theory can afford a valid explanation of the distribution of these warm-water epiplanktonic Copepoda, whereas the older theory of the permanence of the older basins fails to do so.

Dr. A. Tindell Hopwood said that the Tertiary and Recent mammals afford no evidence in favour of continental drift, and that there is little or nothing in their distribution which cannot be explained by the principles enunciated by W. D. Matthew in his essay 'Climate and Evolution' (2nd ed., New York Acad. Sci., 1939). On the other hand, continental drift does afford the most satisfactory explanation of the present curious distribution of the late Carboniferous and early Permian glacial deposits, and also provides a mechanism for the post-Middle Pleistocene earth movements, which not only elevated still further the great mountain ranges of the western Americas, and of the Alpine-Himalayan girdle, but, in addition, powerfully affected various other features such as the great Rift Valley system of Africa.

The explanation of this apparent conflict between the geological and zoological evidence is that the break-up of the two primitive continents of Laurasia and Gondwanaland took place in pre-Tertiary times. Insufficient is known of the Mesozoic mammals to make their evidence concerning that earlier period of any value.

Prof. A. C. Hardy. Whilst I can see so much in the distribution of the lower animals to support the hypothesis of continental drift, I always feel that the mammalian fauna of Australia is a stumbling block. Australia, according to the drift hypothesis, would have been much further from Asia in the Cretaceous than it is today, and in that period, according to Wegener, it and Antarctica were also well separated from Africa but connected with South America. At one time, when *Coenolestes* was thought to be a diprotodont marsupial and when some of the fossil carnivorous marsupials of South America were thought to be allied to forms like *Thylacinus*, it was popular to speak of the Australian mammals being derived from South America via an Antarctic land bridge. Now, when it has been shown that *Coenolestes* is really an aberrant polyprotodont and that the fossil carnivores are of didelphid and not of dasyurid stock, the need for such a land bridge to account for the marsupial distribution no longer exists. Such a connection would not account for the monotremes in Australia. No monotreme remains have been found in South America, and all the evidence points to that continent having received its first mammals from the north in the Eocene. Apart from not explaining the monotremes, if there had been a link between South America and Australia in the Eocene, or later, it would be surprising that some of the other early South American forms, such as the Xenardran Edentates, Notoungulates and Platyrrhine monkeys should not have crossed the bridge with the marsupials. I have not seen this point raised in connection with continental drift, and would like to see it discussed.

Dr. F. E. Zeuner, F.Z.S., said that he had analysed the geographical distribution of certain groups of mammals and insects in the light of the geological history of the Indo-Australian Archipelago; for instance, *Melobasis* (Coleoptera), *Troides* (Lepidoptera) (see Proc. Linn. Soc. Sess. 154, p. 157; Trans. Zool. Soc. Lond. 1943/3). The results are best explained by the assumption that, at the end of the Tertiary, New Guinea lay at least 750 miles south-east of its present position. No other geological or climatological theory would account for the facts of distribution equally well. He agreed with Sir Thomas, however, that

this kind of evidence, strong though it may be, cannot be regarded as of the ' crucial ' class, proving the drift theory as such.

A difficulty of the drift theory which has frequently been neglected is the existence of a latitudinal ocean throughout the major part of geological history, namely, the Tethys. It has been taken into consideration by Du Toit. It might add a complication to the interpretation of Dr. Sewell's interesting work.

Prof. G. D. Hale Carpenter drew attention to the breeding place of the European and American freshwater eels as furnishing one of the strongest biological arguments for Wegener's theory.

Mr. Kailas Nath Kaul, with the aid of the following map, suggested that drift explains the distribution of the two types of floras (temperate and tropical) in Asia from the Tertiary backwards to the Carboniferous period.

Distribution of palms (tropical) in the Tertiary Age : but between the circles fossils suggest temperate climate.

In the Tertiary, in the Americas palms were distributed from lat. 50° N. to 10° S., and in Europe and Africa from 51° 5′ N. to 25° S. ; but in Asia (excepting Japan) otherwise, their place in latitudes north of the Himalayas being occupied by a temperate flora (see Kryshtofovich in ' New Phytologist ', xxviii, p. 303 ; 1929). South of the Himalaya, areas in which fossil palms occur extend west to the Irrawaddy and along the tectonic lines through the Arakan Yomas, the Andamans, Sumatra, Java and Borneo (i.e., on the eastern boundary of Gondwanaland) to New Zealand (Du Toit, ' Our Wandering Continents ', ed. 3, p. 177 ; 1937).

In the Permo-Carboniferous, on the two sides of the above mentioned tectonic lines, *Gigantopteris* flora and *Glossopteris* flora were evolved respectively in two different climates (see Sahni, Journ. Ind. Bot. Soc., XV (5), p. 323 ; 1936).

These two regions are found dove-tailed with each other in our modern map along the Himalayan-Sumatra-Borneo tectonic lines which run zig-zag through different latitudes.

This gives us no escape from the conclusion that the two provinces lay far apart, north and south of the Tethys, and have since drifted towards each other.

Sir THOMAS HOLLAND thanked the members of the two Societies for the privilege of meeting them and of hearing their views, especially from the biological point of view. The contributions generally seemed to be not inconsistent with the theory of drift ; and some of them, like the contribution made by Col. Sewell, quite new.

PROCEEDINGS OF THE GENERAL MEETING
13 May 1943.

held jointly with The Zoological Society of London.

Dr. E. S. RUSSELL, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 8 April 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Professor Wen-pei Fang, Dr. Nicholas Polunin, Miss May Rathbone, Mr. N. Y. Sandwith, Svenska Linné-Sällskapet and U.S. Office of War Information.

Read for the first time certificates of recommendation of the following candidates for Fellowship : in favour of Alec Lindsay Poole, Leon Raymond Hayward and William Homan Thorpe.

Read for the second time certificates of recommendation of the following candidates for Foreign Membership :—Professor Carl Johan Fredrik Skottsberg and Dr. Alfred Ramalho.

Read for the second time certificates of recommendation of the following candidates for Associateship, *honoris causa* :—Thomas William Burton and Charles Biddolph.

The President announced the title of his Presidential Address, ' The stereotyping of Instinctive Behaviour '.

Mr. ANTHONY BELT exhibited an abnormal Tulip with the following characters :—The bulb had produced three flowers ; the terminal flower was outwardly normal ; the first lateral flower had only two carpels ; the second lateral flower had the outermost member of the perianth partly foliaceous.

Dr. E. M. Delf described the phenomenon of aërial tuber-production on the Potato plant, and it was discussed by Mr. D. M. Reid, Mr. A. D. Cotton, Dr. R. Melville, Mr. F. J. Chittenden, Mr. I. H. Burkill, Dr. B. Barnes, Dr. J. Ramsbottom, Lt.-Col. W. P. C. Tenison; Dr. Delf replied.

Dr. Delf said:—In recent years, like a good many others, I have been concerned with growing potatoes and have handled some hundreds of plants of four different varieties. They were all grown on light sandy soil on ground sloping gently down towards a small stream, so that in the lower areas the soil was much moister, owing to the higher water-table.

Last summer, in these lower regions, a considerable number of plants (race 'Majestic') bore aërial tubers on the lower parts of their stems, to a distance of some 8–10 inches above ground. Morphologically, there were four types:—(1) Tubers formed singly in the axils of the lower leaves; (2) two or even three small tubers in the same leaf axil, because supernumerary axillary buds were also tuberized; (3) slender axillary shoots with tubers along their length, at the nodes; and (4) axillary shoots swollen at the base, tapering to the apex, forming pear-shaped structures. All these aërial tubers were green or greenish in colour.

As the yield of underground potatoes of these plants was quite good, it was thought that the cause of the formation of aërial tubers lay in the damp soil and rather straggly overgrown shoots, but a number of specimens of the same race, 'Majestic', were in the same season obtained by Dr. Polunin at Oxford, showing aërial tubers (Types 1 and 2 above), although his plants came from a light soil in a dry situation. It is therefore suggested that this may be a racial feature, provoked by factors which have apparently not been analysed.

Mr. D. M. Reid said that aërial tubers had been common in northern Scotland during the last wet summer.

Mr. A. D. Cotton said that the production of aërial tubers in potatoes was often associated with injury at the base of the stems, either of a mechanical nature such as that caused by wind, human or animal agencies, or by injury due to a disease such as a mild attack of Blackleg. He had examined a number of specimens and had come to the conclusion that in such cases the phloem tissues were injured and that the downward passage of carbohydrates was obstructed. The carbohydrates tended, therefore, to accumulate in the stems, and this led to tuber production from the buds in the leaf axils of the particular stems damaged. He felt certain that injury was the usual cause of the phenomenon, but it might perhaps be brought about by other means. If a very large number of plants in a field were concerned the possibility of the variety being susceptible to a specific disease should be borne in mind.

Dr. R. Melville said that he had observed aërial tuber formation on several races of potato. They tended to develop when earthing up was not done, the stolons did not then elongate and short lateral branches developed directly into tubers. There was also the possibility that virus diseases may favour their development. It was known that some virus diseases disorganized translocation and caused the accumulation of carbohydrates in the aërial parts. This may favour aërial tuber formation.

Mr. F. J. CHITTENDEN said he had seen many examples of potatoes bearing tubers on their aërial stems, usually axillary in the lower part, and in most cases where he had examined them had found damage to the stem tissues below the tuber-bearing part, and had come to the same conclusion as Mr. Cotton. He had, however, received in 1941 a plant from a garden in Petworth bearing a very large number of aërial tubers throughout the stems (whether damaged below he could not say) not only in the leaf axils but also in the inflorescence. He showed a photograph of part of the plant. It was difficult to account for the tubers in the inflorescence unless one assumed there was a considerable upward, as well as the usual downward, movement of carbohydrates made in the leaves.

Mr. I. H. BURKILL suggested that polarity is involved and that various external forces may play on it, adding that man had been able, overcoming the polarity, to select races in the genera *Dioscorea* and *Allium* in which the formation of bulbils above ground normally replaces the formation of tubers or bulbs underground.

Dr. B. BARNES remarked that he had several times seen aërial tubers in potato, and that they had appeared casually on odd plants among many quite normal plants. He also referred to the experimental induction of such tubers by Vöchting.

Lt.-Col. W. P. C. TENISON said that he had often seen aërial tubers in the potato fields of Co. Monaghan, Ireland, where they are always regarded as poisonous.

Dr. DELF, replying in the discussion, said that it had brought to light points of considerable interest, suggesting the complexity of the factors involved in the formation of aërial tubers. She continued : With regard to the suggestions that translocation had been inhibited or slowed down by failure to earth up, or by injury of some kind (mechanical or biotic), if this occurred in my plants, it did not prevent the formation of a good number of well-formed subterranean tubers on the same plants.

I was interested in the illustration of Vöchting's apparatus given by Dr. Barnes. A good many years ago I procured a similar dark box and tried to emulate Vöchting's results but without success, perhaps owing to the atmosphere of the box being too dry or perhaps owing to lack of vigour in the experimental plants.

Dr. ANNIE PORTER gave an account in the names of the late Prof. H. B. FANTHAM and herself of *Plasmodium struthionis*, sp. n., from Sudanese Ostriches and *Sarcocystis salvelini*, sp. n., from Canadian Speckled Trout (*Salvelinus fontinalis*), together with a record of a *Sarcocystis* in the Eel Pout (*Zoarces angularis*).

Abstract.—

Special interest attaches to avian malarial parasites, as the first life-history of a malarial parasite in its insect vector was worked out by Ronald Ross on an avian form, the results being applied by him to the malarial parasites of man and their Anopheline transmitters, with far-reaching results. Bird Plasmodia are now much used in the chemotherapy of malaria. Many species of Plasmodium from a variety of birds have been described, of which twelve are admittedly valid.

Plasmodium struthionis is now described from Sudanese ostriches, *Struthio camelus*. Young 'ring' stages, schizonts forming eight merozoites and small, oval macrogametocytes and microgametocytes have been found. The parasite level is low. Deformation of and nuclear displacement in the erythrocytes were caused by the parasites. The transmitter could not be determined. Detailed comparison with valid species of avian Plasmodium showed distinct morphological and dimensional differences. The nearest affinity appears to be a much larger, unnamed Plasmodium of the emu (Carini and Maciel, 1916). As the hosts belong to nearly related families, their Plasmodia may prove to belong to a small natural group in which differences have arisen by geographical separation and isolation of the respective hosts.

Sarcosporidia, hitherto recorded from Primates, Ruminantia, Rodentia, Aves and Lacertilia, are now described from Pisces, e.g., the Canadian *Salvelinus fontinalis* and *Zoarces angularis*. *Sarcocystis salvelini* occurred in one speckled trout, the abdominal muscles anterior to the anus being affected and marked muscular breakdown being produced. The largest sarcocysts were about 0·5 mm. long. All stages up to spore formation and mature spores were found by microdissection, fresh preparations and sections. The dimorphic spores were 5·2–8·8 μ by 1·5–2·5 μ. It was shown that dimensions and morphology, as well as host, separated them from known species. Another much larger, different species of *Sarcocystis* is recorded from the eel pout, *Zoarces angularis*.

Dr. Carmichael Low congratulated Dr. Porter on her very interesting paper. Parasites were found throughout the animal kingdom, from man downwards, he said, and the genus *Plasmodium* was a very important one, as it included the malarial parasites of man. Those present, no doubt, remembered how Sir Ronald Ross elucidated the spread of malaria from man to man by the way of an intermediate host, the mosquito. Working with the malaria of sparrows in India he was able, by feeding mosquitoes upon them, to show that their parasites underwent a development in the insect, which eventuated in forms which were injected back into other birds and so spread the disease. This work, applied to human malaria, showed that a similar development took place, though in a different kind of mosquito, namely, an *Anopheles*.

In Dr. Porter's pictures one saw forms which were described as microgametocytes and macrogametocytes; the former being the male element, the latter the female. When these were taken up from the blood by mosquitoes they were carried to the stomach and the microgametes gave off flagella (=the spermatozoa of higher forms of life) which penetrated the female spheres and so produced sexual union. Changing shape now into what were known as travelling vermicules, the bodies penetrated into the walls of the stomach and came to rest there as oocysts. In these oocysts development took place, and finally they became packed with bodies known as sporozoites, which, when the cyst burst, escaped into the tissues of the mosquito and finally were collected by the salivary glands. When the mosquito next bit these were injected into the host, and so produced the disease. The asexual development in the host Dr. Porter had already described.

One of the most fascinating points in the study of *Plasmodia* of birds and other animals was that of discovering the different intermediate hosts required for their development, but this was by no means an easy matter, as to be certain one had to rear batches of clean insects to work on.

The paper, with plate, will be published in full in the ' Proceedings of the Zoological Society of London '.

Mr. J. Pryce-Jones read a paper on ' Some problems associated with Nectar, Pollen and Honey '. (Communicated by Dr. E. M. Delf. Discussed by Mr. H. A. Hyde, Dr. R. Melville, Mr. Cartwright Farmiloe, Dr. Malcolm A. Smith and Dr. B. Barnes.) [Printed in full below.]

SOME PROBLEMS ASSOCIATED WITH NECTAR, POLLEN AND HONEY.

By John Pryce-Jones.

The art of bee-keeping has been practised from remote antiquity, but no advances of fundamental importance were made until the middle of the nineteenth century, when Langstroth invented the movable-frame hive and Hruschka discovered the principle of honey extraction from the combs. These two ideas laid the foundation of modern keeping and the gradual development of commercial apiaries throughout the world. Bees are kept in order to obtain honey, but it is not generally recognized that the value of bees as pollinators of orchard and farm crops greatly exceeds the value of the surplus honey they produce. It is estimated that the annual value of bees as pollinators in England and Wales is at least £4,000,000, whereas the value of the honey is barely a third of that figure.

It may seem rather out of place that a physical chemist should address a gathering of biologists on the relationships which exist between bees and flowers, and on the problems related to nectar and pollen which still need attention. I therefore wish to emphasize that my purpose is not to instruct but to remind you of a number of interesting facts in the bee-flower relationship which require explanation. Those of you who are in academic life will find a number of problems associated with nectar and pollen which will not only provide your students with the subject for a thesis, but which will provide them with an interesting hobby for the rest of their lives. As in many other sciences, apiculture owes a great deal to the labours of amateurs, and I may call your attention to the names of three distinguished men who devote their leisure time to the development of apiculture—Wedmore, an electrical engineer; Frow, a railway official; and Yate Allen, a country clergyman. Neither must we forget the name of Tickner Edwardes, the author of two famous classics which have greatly influenced the development of bee-keeping throughout the English-speaking world.

The title of this lecture hardly lends itself to a formal treatment. I therefore propose to adopt a discursive method of presentation, so that you can relate the facts to the general background of your own experience and expert knowledge, and I hope that the problems they suggest will be of more than passing interest to you.

The bee–flower relationship.

The life of the bee is dependent upon nectar, pollen and water, and the first two can be derived only from plants and flowers. A flourishing colony of bees contains from 40,000 to 50,000 bees and they need about 400 pounds of honey and about 40 pounds of pollen per annum to supply them with food and warmth and for the synthesis of wax for their combs. The surplus honey, that is the honey available to the bee-keeper, is only about 50 pounds per colony per annum in Great Britain, although a surplus of 200 pounds or more is occasionally obtained. Of course, in the great honey-producing countries of the world much greater yields are obtained, and an average of 120 pounds per colony per annum is quite usual in some of the northern parts of the United States. As the honey sac of a bee has a capacity of about 0·025 cubic centimetres, this means that 20,000 flights of a bee are required for the collecting of a pound of nectar or 80,000 flights for collecting a pound of honey.

Nectar provides the bees with carbohydrates and minerals, and possibly traces of vitamins, and pollen provides proteins, fats, minerals and vitamins. It is, therefore, obvious that plentiful supplies of both nectar and pollen are essential for the needs of the colony. In normal times plants supply abundance of both foods.

Bees also gather propolis. As far as is known it has no food value, and is not an essential factor in the bee–flower relationship. It is used by the bees as a lute and in sealing cracks and for strengthening combs. It is a mixture of resin and vegetable wax, collected from trees and shrubs from which it freely exudes at certain seasons. We need not concern ourselves with this material beyond stating that its most important aspect in bee-keeping is its deleterious effect upon the colour of wax. It may also be mentioned that it is used in Germany as a healing balm, and that it is reputed to have been used by Stradivarius and other violin makers in Cremona as a violin varnish, where it was found in abundance on the local poplars.

In passing, it may be mentioned that the process of wax secretion by the bees is still a mystery. Virgin wax is pure white and it derives its colour from pollen and propolis as well as from the processes involved in its recovery from the combs.

Nectar is secreted by plants from floral as well as extra-floral nectaries and its true function in the life of the plant is not clearly understood. It is generally accepted that nectar is secreted in order to attract insects and that plants are so designed that in the act of gathering nectar the insect covers itself with pollen which it transfers from flower to flower and thus brings about cross-pollination. As cross-pollination is an important factor in the survival and evolution of plants, it is believed that secretion of nectar along with brilliant colours and attractive scents are methods designed to ensure this process by the aid of insects which are correspondingly endowed with highly developed senses of taste, colour and scent. It is unnecessary here to describe the numerous beautiful examples in nature which appear to confirm this teleological view of the secretion of nectar ; but it should be realized that all the facts relating to the origin and composition of nectar do not support this theory. At present we need only ask : What is the teleological

argument for extra-floral nectaries? We will return to this question later. There are others who believe that the function of nectar is the drawing away of water from the anthers by osmosis, thus to accelerate the liberation of pollen after wet weather. Insects encourage this process by removing the nectar and thereby maintain the concentration of sugar in the cell sap. According to this view nectar serves only a secondary purpose in attracting insects for carrying pollen. Irrespective of any theories which we may propose for the purpose of nectar in the life of a plant, it is universally agreed that insects are extremely efficient pollinating agents.

Bees collect pollen for the hive by two more or less distinct methods. The first method rests on the collection of nectar during which the bee gathers pollen as a supplementary load, and does not deliberately set out from the hive to gather pollen. In the second method the bee deliberately gathers pollen from a flower which may or may not be a source of nectar as well, but the pollen gatherer pays no heed to the nectar, as it purposely takes on its flight a small amount of honey in order to moisten the pollen, and thus facilitate its packing in the pollen baskets. (If the bee is primarily gathering nectar it moistens the pollen with nectar.) Although most pollens contain the foods essential for bees, we shall see later that bees select pollen according to their own 'tastes', and it appears that the process of selection is based upon the relative abundance of certain materials in the respective pollens.

Definition of honey.

The worker bees collect nectar from flowers and carry it back to the hive in their honey sac, where it is passed on to the home bees, who ultimately transfer it to the cells, where it is ripened and stored as honey. After examining many hundreds of samples of honey from most parts of the world, I am convinced that its most characteristic feature is its infinite variety. Although most honeys are pleasantly sweet, a large number are distinctly bitter and undesirable. They vary in colour from the water-white honeys of *Fuchsia* and willow herb (*Epilobium*) to the dark brown heather (*Calluna*) and buckwheat (*Fagopyrum*) honeys; in viscosity from the thin honey from the dandelion (*Taraxacum*) to the vining milkweed honey (*Gonolobus laevis*) which almost refuses to flow from the combs in an extractor; from the rapidly granulating honey from charlock (*Brassica arvensis*) to the tupelo (*Nyssa* sp.) and purple sage (*Salvia spathacea*) honeys which remain liquid almost indefinitely. These are only a few of the more obvious differences, a great many others can be observed by the delicate methods of physical and chemical analyses.

It would appear, therefore, that it is not an easy matter to formulate a satisfactory definition for honey, but for an ideal definition we may say: 'Honey is a concentrated sugar solution prepared by bees from the nectar of plants'. This definition does not embrace all honeys, as the bee often gathers and stores honeydew in its combs. As a practical definition we can therefore adopt the following: 'Honey is a concentrated solution of sugars prepared by bees from the sweet juices of plants'. Honeydew is a secretion from various aphids,

and is collected by bees from a great variety of trees, such as pines, cedars, limes, firs, oaks, willows and sycamores. This very dark sample shown here is the honeydew obtained from the incense cedar (*Libocedrus decurrens*) of California. In general, we shall confine our attention to honeys which do not contain honeydew, as the latter is not a true secretion.

The conversion of nectar into honey.

Nectar is essentially a dilute solution of sugar in water ; the most abundant sugar is sucrose, but certain nectars contain appreciable amounts of glucose and laevulose as well. After the bee has transferred the nectar from the flower to its honey sac it adds a trace of invertase, which is an enzyme, and this converts the sucrose into a mixture of equal parts of laevulose and glucose. The nectar containing a trace of invertase is ultimately transferred to the cells in the combs, where, after a period of three days in the heat of the hive, it is converted into honey. The cells are then capped with a layer of wax and stored for time of need. The process of converting nectar into honey is called 'ripening' and consists of the formation of laevulose and glucose from the parent sugar, sucrose, and the evaporation of water. The change can be represented in the following way :—

Nectar.		*Honey.*	
Water	75 per cent.	Water	20 per cent.
Sucrose	25 ,,	Laevulose ...	40 ,,
		Glucose	40 ,,

If the above were a true and complete description of the nature of nectar and its conversion into honey it would follow that all honeys from the vast number of plants would represent one uniform and uninteresting product. The dozen samples exhibited here show that honeys are most variable in their properties, so that it is essential to modify this simple illustration and examine our honeys in greater detail. It is natural to assume that as honey originates from nectar, the composition of the honey gives us a fairly clear insight into the composition of the parent nectar after making allowances for the evaporation of water. (Thus we can assume that the ratio of potassium to sodium as determined in honey is the same as it was in the parent nectar.) Analyses of a large selection of honeys reveal that they contain gums, tannins, dextrins, enzymes, essential oils, esters, mineral salts, acids, yeasts, proteins and traces of vitamins. These substances are found in normal honeys, and the list does not include the constituents found in abnormal honeys such as those of *Arbutus Unedo* or *Rhododendron ponticum*. As all these various compounds are found in honey, they must also be present in the parent nectars, apart from traces which originate from pollen and the bee ; thus it is probable that honey diastase is derived from pollen, and that most of the acids in honey, as well as the invertase, is derived from the bee ; although none of these three assumptions has so far been proved. Naturally some of the minor constituents of certain honeys—for example methyl anthranilate, found in orange honey (from *Citrus* spp.)—are characteristic of the parent plant and its fruit, and we shall meet with other examples in the sequel.

Some typical analyses of honeys.

Floral source.	Water.	Dextrin.	Ash.	Undetermined.	Sucrose.	Laevulose.	Glucose.	L/G.
	%	%	%	%	%	%	%	
Alfalfa ..... (*Medicago sativa*)	14·84	0·06	0·12	4·50	1·14	41·20	38·0	1·08
Apple ..... (*Pyrus Malus*)	19·65	1·24	0·32	6·26	1·46	41·00	29·91	1·37
Blue Curls ..... (*Trichostema lanceolatum*)	17·86	0·27	0·12	2·55	3·13	35·70	40·34	0·88
White Clover ..... (*Trifolium repens*)	16·60	0·12	0·07	4·49	1·12	41·00	35·90	1·16
Fleabane ..... (*Erigeron* sp., not *Inula*, as in Britain)	16·12	11·91	1·14	5·86	4·30	34·50	26·02	1·33
Hyssop..... (*Agastache nepetoides*)	16·58	8·97	0·81	2·76	5·72	40·00	24·25	1·63
Orange ..... (*Citrus* spp.)	16·00	0·19	0·14	6·48	1·83	42·40	32·83	1·21
Purple Sage..... (*Salvia spathacea*)	16·36	0·84	0·08	6·45	1·46	43·80	30·92	1·42
Star Thistle ..... (*Centaurea* sp.)	15·45	0·73	0·19	4·86	4·38	40·40	33·71	1·20
Tupelo ..... (*Nyssa* spp.)	17·26	1·04	0·27	4·48	1·62	47·93	27·40	1·75

(All the above analyses, apart from the tupelo figures, are taken from Bulletin 631 of the College of Agriculture of the University of California by J. E. Eckert and H. W. Allinger.)

The fleabane and the hyssop honeys contain an appreciable amount of honeydew, as shown by the exceptionally high proportion of dextrin which is one of the chief characteristics of this substance. They also contain appreciable amounts of the trisaccharide sugar, melezitose, which is secreted by plant aphids and which is not converted into laevulose and glucose by honey-bees; in the above figures this sugar is probably included under sucrose. It is not proposed to discuss honeydew in detail in this lecture, but the two analyses were included in order to show the effect of the presence of honeydew on the composition of honey. The following comments refer to the pure honeys listed in the above table.

It is evident that very wide variations are observed in several of the constituents, and perhaps the most significant are those described as 'Undetermined'. It is highly desirable that these undetermined products should be examined in greater detail, as they will probably reveal significant peculiarities in the method of secretion of nectar or in the metabolism of the plant. The origin of honey 'dextrins' is still unknown and their constitution is not clearly understood because they do not consist of normal dextrin; the variation in colloid content is of particular interest, as these variations must reflect differences in the structure of the nectary membranes. As already mentioned, the conversion of

sucrose into laevulose and glucose should lead to the formation of equal parts of these sugars, or, in other words, the ratio L/G should be equal to 1. In the table it will be seen that the ratio varies from 0·88 for blue curls (*Trichostema lanceolatum*) to 1·75 for tupelo (*Nyssa* spp.), hence these pa[illegible]ed nectars cannot be composed of sucrose alone, but must also contain appreciable amounts of laevulose and glucose. (We may quote a recent paper by Vansell, in which he showed that certain orange nectars contained : sucrose, 11·45 per cent ; laevulose, 5·97 per cent ; and glucose, 5·6 per cent.) It would be of great interest if we could determine why certain plants secrete nectar which yields the theoretical ratio of 1 and others yield honeys with such different ratios. The differences in the laevulose glucose ratios have a very important practical aspect, as they determine to a very large extent the rate of granulation of honey. It may be accepted that honeys with low ratios, such as the clovers, granulate quickly, whereas honeys like tupelo and purple sage (*Salvia spathacea*), which have a very high ratio, remain liquid almost indefinitely. The recent policy 'plough up the fallow land' has led to a profuse growth of charlock (*Brassica arvensis*) in many parts of Britain, with the result that many bee-keepers have found that their honey has crystallized almost as soon as it was extracted from the combs, for the reason that charlock honey has a very low laevulose/glucose ratio.

The variation in ash content is also of importance ; the mineral salts present in honey are, naturally, the same as those in the cell sap, but the ratios of the elements present in honey, and, therefore, in nectar, differ considerably from the ratios of the same elements in cell sap, and no doubt these differences are due to the selective permeability of the nectary. Schuette, for example, has shown that there are wide variations in the iron, manganese and copper contents of honey, and that the amounts of these elements greatly influence the colour of the honeys. No systematic attempt has been made to correlate the quantity and quality of mineral salts in honey or nectar with the plant habitat, but in 1939 I made a preliminary examination of the soluble salts present in about 80 samples of various honeys by the method of electrical conductivity. This method is a simple, but approximate, test of the soluble salt content of honey, and very interesting curves are obtained by measuring the conductivity at various degrees of dilution, as it depends on viscosity as well as soluble salts. The detailed results will be published at some later date, but it is of interest to state that samples of white clover and sainfoin (*Onobrychis*) honeys showed the lowest conductivities ; and samples of bell heather (*Erica*), ling (*Calluna*) and buckwheat (*Fagopyrum*) showed the highest conductivities. It is also significant that samples of clover from the Cotswolds, Wiltshire, New Zealand, Canada and Mexico, and various other sources, all had practically the same conductivities ; the same is true of samples of ling honey from Yorkshire, Devon, Ayr, Sutherland, Brittany, Sweden and the Luneberg heath in Germany. It would therefore appear that the amount of soluble salts in the nectar of plants is a characteristic of their natural habitat, and that it is much higher in plants which grow in soils of low *p*H value than in plants, such as clovers, which require an alkaline soil of higher *p*H value. It is hoped to continue this work with a much

greater variety of honeys as soon as samples are available after the War. It will also be of great interest to compare the quantitative composition of the ash of various honeys with the ash of the parent cell sap, and in this way attempt to determine the factors which influence the selective permeability of the nectaries.

It may be of interest to mention that a great many bee-keepers believe that when bees are fed on sugar syrup—as they are in times of shortage of stores and nectar—the bees merely concentrate the sugar syrup, but do not convert the sucrose into honey. This is quite a mistaken idea; along with many others, I have proved that bees convert sugar syrup into laevulose and glucose and that the resulting honey contains a considerable amount of excess invertase—as is found in honey derived from nectar. The United States Bureau of Entomology recently carried out an interesting series of experiments, during which they showed that certain nectars when kept for a year or more are converted into a solution of glucose and laevulose without the addition of invertase.

Poisonous honeys.

Although there has been a general impression for a long time that certain honeys are poisonous to man, it is a matter of considerable difficulty to obtain convincing evidence on this belief. References are frequently made in the bee-keeping journals to sudden illnesses stated to have been caused through the eating of poisonous honey, but when a competent chemist has carried out a complete examination of the remainder of the sample of honey the results give no indication of the presence of a poison. These remarks, however, do not preclude the existence of poisonous honeys, and a recent remark by Miss Betts is of importance in this connection. She states that, along with several others, she ate a portion of a comb of honey and suffered rather serious effects, although the others, who shared the comb, experienced no ill effect. We must accept the opinion of such an eminent authority as Miss Betts when she offers the explanation that it is possible that the bees store the abnormal honey in separate cells and that the amount is sufficient to fill a few cells only. This theory would explain her experience, which is similar to that of several others who have suffered ill effects from eating a portion of a honeycomb.

The earliest description of poisonous honey is that given by Xenophon, who states that when his army was encamped at Trebizond, on the shores of the Black Sea, in 400 B.C., a great number of his soldiers were taken seriously ill after eating the honey of *Rhododendron ponticum*. It should be pointed out that the honey was found in hives and not in the honeycombs of wild bees. It is interesting to recall that Kingdon Ward describes a similar experience in 'A Flower Hunter's Paradise', when his porters were taken ill after eating wild honey, which also was derived from the same genus. Archangelsky, in a paper which I have seen only in abstract form, claims to have discovered two new toxic substances, allied to camphor, in *R. ponticum*, and which he has called rhododendrin and ericolin. It may be mentioned that the most frequent references to honey stated to be poisonous relate to the regions around the Black and the Caspian Seas.

The ancient writers often referred to poisonous honeys: thus Virgil describes the poisonous honey from Corsican yew trees and Pliny mentions the dark-red goat's-bane honey which induces violent sneezing and convulsions. It is well known that certain Turkish honeys contain saponins, so that it is possible that Pliny had met similar honeys, as saponin, under certain conditions, is known to produce sneezing.

In America it is believed that the honeys of mountain laurel (*Kalmia latifolia*) and of yellow jessamine (*Gelsemium sempervirens*) are strongly poisonous: but no authoritative medical or chemical evidence supports this belief. It is known, however, that, when grown in certain localities, the jessamine is poisonous to rabbits.

Although we cannot definitely accept that there are honeys which are actually poisonous to man, there is abundant evidence that certain honeys possess highly undesirable flavours and a bitter taste. Thus the honeys from *Helenium autumnale* and *H. tenuifolium* possess a distinctly bitter taste, and the honey from chinquapin (*Castanea nana*), according to E. R. Root, tastes like a mixture of quinine and cayenne pepper.

One of the most familiar of these bitter honeys is Noors honey, which was exhibited at a meeting of this Society some years ago, from the Sunday River Valley in South Africa. (Robert Moffat, in his 'Missionary Labours in South Africa', describes poisonous South African honeys.) Noors honey is gathered from certain species of *Euphorbia* which grow in abundance in the Sunday River Valley. Juritz, of the South African Agriculture Department, states 'a small portion of the honey was tasted and after a few minutes there was a burning sensation in the throat and a distinct feeling of nausea. The effects did not wear off for several hours'. The analysis of the honey was normal apart from the presence of the excessive amount (10 per cent) of non-sugar solids. Juritz was able to extract the bitter principle as a solution in ether, and he obtained an extract with a similar taste from the dried flowers of certain species of *Euphorbia*. I examined a very small sample of Noors honey and obtained sufficient ether extract to confirm the observations of Juritz, but was unable to identify the bitter principle.

It is stated that the honey from *Spirostachys Johnstonii*, which grows in Swaziland, imparts temporary insanity, but I have no direct evidence on this statement.

From the neighbourhood of Gallura, in Sardinia, is gathered a honey of lemon-yellow colour and aromatic odour which is intensely bitter to the taste. It is obtained from the strawberry tree, *Arbutus Unedo*, named 'unedo' by Pliny because the taste of one berry of this tree is sufficient. This honey contains the glucoside arbutin, which is a compound of glucose and hydroquinone, and its presence can readily be shown by standard chemical tests—for example, after appropriate treatment a beautiful azure colour is produced by ferric chloride and an intense sapphire colour by Youngman's reagent. The bitter principle was first identified by Sanna at the University of Ragusa, and I confirmed his observations at a later date. It is evident that convincing evidence can be obtained for the presence of some abnormal constituent in the honey of *Arbutus Unedo*, and it is desirable that a systematic

analysis should be made of all honeys which are alleged to be poisonous, or to possess an undesirable taste, with a view to corroboration by analysis of its origin from the parent plant.

A number of other honeys which I have not named possess bitter tastes, but these few examples are sufficient to indicate that this property is a feature of certain honeys. Further evidence that there are plants which secrete abnormal nectars is given in the following paragraph.

Nectar poisonous to bees.

Vansell and Watkins report two very interesting cases of nectar which is poisonous to honey-bees. The first concerned some colonies in the Mason Valley in Nevada in the summer of 1933, when bees were found dying on the blossoms of loco-weed (*Astragulus lentiginosus*). Not all the visitors to the plant are visibly affected while gathering the nectar, but many bees drop on the return flight to the hive, or, if they reach the hives, they are too weak to enter and soon expire. Bees do not normally work on loco-weed, but do so during dearth of clover and when the desert flora is the only source of nectar until the second alfalfa crop begins to bloom. As soon as any other attractive source of nectar is available the bees abandon the loco-weed, and the colonies become quite normal when removed to other pastures. The second case was found in the high Sierra Nevada mountains in Eldorado County, where bees were found dying, at the rate of about 50 per minute, when returning to one particular hive. The dead bees were found in a curled attitude, as if they had been stung by other bees. The colonies left in the valleys were perfectly normal. The high death rate continued until buckwheat brush (*Eriogonum umbellatum*) came into bloom and the bees were able to obtain a source of nectar close to the hives. It was revealed that the source of the poisonous nectar was the plant western false-hellebore (*Veratrum californicum*), growing about 1,000 feet above the hives, as numerous dead bees were found on the blossoms. Each leaf of this plant forms a sheath-like cup about the stalk below the terminal panicle of blossoms. The uppermost of these receptacles was found to contain the dead bodies of numerous insects, other than honey-bees, such as ants, beetles and flies. The plant is known to be poisonous to stock, but is considered unattractive to bees. The plant is found usually on mountain meadows, from northern Washington, eastwards to Colorado and south to Mexico.

It may be mentioned that Californian buck-eye (*Aesculus californica*) is also poisonous to bees; and Vansell has reported that he has seen dead bees in front of single colonies to the depth of three or four inches after foraging on buck-eye blossoms. The nature of the poisonous substances in these nectars has not been discovered; it has been suggested that it may be due to selenium, which is absorbed by various plants in certain localities, as it is known that the presence of selenium in plants is poisonous to cattle.

In Central Europe the nectars of certain milkweeds (Asclepiads) are poisonous to bees; it is therefore of interest to state that a highly toxic material, galitoxin, has recently been isolated from the flowers of the milkweed, *Asclepias galioides*.

C. G. Butler, at Rothamsted, has commented on the fact that there is apparently a close association between a period of drought in the summer and serious outbreaks of certain forms of bee paralysis. Such an outbreak occurred during the months of June and July 1942. Although not strictly associated with nectar, but with honeydew, the observations are described here because of their inherent interest and their importance to bee-keepers. In districts where such outbreaks occurred it was found that a large number of bees were working on the leaves of various trees such as lime, beech, oak and sycamore in search of honeydew excreted by Homoptera thereon. Separate samples of honeydew were collected from the various species of trees and fed to bees kept in separate cages. The honeydew from lime (*Tilia platyphylla*) was found toxic to the bees even when highly diluted with water. Bees which had been fed on diluted solutions of this substance all died within eight hours, and their symptoms were similar to those which suffered paralysis by gathering honeydew from the trees. It was found that neither boiling, nor filtering, nor evaporation to dryness and subsequent solution and filtering removed the toxic substance from the lime honeydew. It was therefore assumed that this particular form of bee paralysis is due to a heat-resistant water-soluble material contained in honeydew excreted by Homoptera on the leaves of the lime.

The problem of ling honey.

The honey from the ling (*Calluna vulgaris*) is unique amongst all honeys gathered in Great Britain, as it cannot be removed from the combs under the influence of centrifugal force in a honey extractor. The combs have therefore to be crushed in a ' heather press ' provided with a layer of filter cloth through which the liquid honey flows, and is thereby separated from the solid wax. As the cell structure of the comb is destroyed in the operation the bees must therefore build new combs for the next season's harvest of nectar. It is of interest to recall a quotation from Frank Cheshire's famous book on ' Bee-keeping ', dealing with the peculiarities of ling honey :—' The beautiful rich-coloured and highly flavoured honey obtained from the heather, the pride of the Scottish Hills, is, for two or three days following gathering, extremely limpid, dropping on the slightest jar from the combs, if the latter are held in a horizontal position, yet it becomes so gelatinous when ripened that the contents of a single cell, if successfully removed, will retain its hexagonal figure for some time, and this apparently from the presence of one or other of the pectose group of bodies allied to arabine '. This passage is of great historical interest because Cheshire describes the precise condition which prevents ling honey from flowing out of the combs when rotated in an extractor. Ling honey, in the language of colloid chemistry, possesses the property of *thixotropy*—that is, the property of certain liquids to set into a jelly when left at rest and of passing again into a liquid when shaken, and of setting anew when left to rest again. Thixotropy is a distinctive characteristic of a great many colloidal systems and plays an important part in many biological processes.

In 1930 I began an extensive series of experiments on ling honey from various parts of Europe in the hope of identifying the particular substance which imparts this peculiar gelatinous property to ling honey. So far I have examined over 300 samples of ling honey, and I am now convinced that the property arises from the presence of a protein which is readily precipitated either by heat or by the addition of various reagents such as alcohol, tannic acid or tri-chloracetic acid. Good quality ling honey contains from 1·3 to 1·5 per cent of protein, and the richest sample I have examined came from the Dartmoor region and contained 1·86 per cent of protein. (Ordinary honeys contain only about 0·2 per cent of protein.) By delicately controlled chemical processes the protein can be removed from ling honey—which thereby loses its thixotropic properties—and be transferred to clover honey, to which it imparts the characteristic thixotropic features of ling honey. Many other chemical and physical methods confirmed that the properties of ling honey were due to the presence of a protein, and an extensive search was then made in various parts of the world for another honey which resembled ling honey. After a long period I found that the manuka (*Leptospermum scoparium*) of New Zealand was highly thixotropic, and this was also observed by my friend Dr. Scott Blair at Rothamsted almost on the same day, and it is probable that we examined the same delivery from New Zealand. I also found thixotropy in a much lesser degree in blue gum and malekeula (Eucalypts) from Australia (but as both these samples contained pollen grains from manuka, perhaps the observations are not significant), as well as in buckwheat honey from New York State and from Brittany; in buckwheat honey the phenomenon is not very marked until the honey has been heated. Examination of manuka honey showed that it contains from 0·6 to 1·0 per cent of protein, which has identically the same reactions as the protein from the ling honey. Although the iso-electric point of both honeys is the same, *p*H 4·2, I am not yet prepared to state that both honeys contain the same protein. Protein solutions show the property of flow-birefringence when observed in a state of strain by means of polarized light. At the beginning of the War, Dr. John Edsall, of Harvard Medical School, kindly examined a sample of ling honey by this method and showed the presence of flow-birefringence, and it is hoped at some later date to continue this work and that it will lead to the identification of the proteins in manuka and ling honeys.

The honeys from *Erica cinerea* and *Erica vagans* from Goonhilly Downs in Cornwall are not thixotropic and they contain only the normal amounts of protein.

It is difficult to explain the presence of these abnormal amounts of protein in ling and manuka honeys. I have tentatively suggested that in the ling it may be associated with the mycorrhiza which play such an important part in the life of this plant. It would be of interest to know whether mycorrhiza or other fungi are essential for the growth of manuka.

Mr. Paul Espinasse has suggested that it is necessary to establish that the protein is definitely of vegetable origin and that it is not produced by the pharyngeal glands of the bee.

The problem of Eucalyptus ficicola.

Eucalyptus ficifolia grows abundantly in the neighbourhood of Stellenbosch, in South Africa, and yields large supplies of nectar. In 1935 I received a small sample of this honey and found that it shows in a marked degree the property of ' Spinnbarkeit '—that is, the property of forming threads or fibres. Pollen analysis by Yate Allen showed that the grains were derived mostly from *E. ficifolia*, and I verified these observations when several clusters of the flowers from the plant were received from South Africa. I have also observed the same property in honey from *Opuntia Engelmanni* from West Africa. Apparently the honey from another Eucalypt, the Gippsland stringy bark, which grows in Queensland, is also spinnbar, as it forms long strings which slow down the extractor when the honey is separated from the comb. From fresh samples of *E. ficifolia* it is possible to draw threads many feet in length ; the sample shown here has been warmed several times during the last five years and is no longer highly spinnbar.

I have shown that the honey from *E. ficifolia* is also dilatant—that is, its viscosity increases with increasing rate of shear, whereas the viscosity of ordinary honeys, such as clover, sainfoin or willow herb, is constant for all rates of shear ; on the other hand, the viscosity of heather honey decreases with increasing rate of shear. Dilatancy is well illustrated by a dispersion of starch grains in an equal weight of water ; such a dispersion, if stirred slowly, resembles a true liquid, but if stirred rapidly it increases in viscosity and bears many resemblances to a solid. The dispersion also shows ' Spinnbarkeit ' to a high degree.

A portion of the honey was sent to Schofield and Scott Blair, who showed that the fibres, when drawn on the surface of mercury and then released, were contractile. The same effect can be observed by drawing a string of honey from a container on the end of a glass rod ; as the string breaks a small liquid sphere is formed, and this ascends to the tip of the glass rod as the string contracts.

So far we have not been able to determine the cause of ' Spinnbarkeit ' in honey. The property is usually associated with liquids of very high viscosity, but the viscosity of *E. ficifolia* honey is not as high as many honeys which do not possess this property. It is probably due to a small amount of a colloidal substance of high molecular weight, and it would be of interest to explain why such substances are secreted in the nectar of certain plants.

The yield of nectar from a plant.

The quantity of nectar secreted by a plant varies from day to day, and even from hour to hour, during the period of flow. As nectar is a solution of sugars in water it is necessary to determine not only the weight of nectar but also the concentration of sugars in the nectar. The amount of honey produced evidently depends both on the quality and the quantity of nectar ; the quality of the nectar (expressed in terms of its sugar concentration) has also a very important significance in the selection of flowers visited by the bees.

Since the introduction of the refractometer method for the direct estimation of sugars in nectar by O. W. Park, of Ames, Iowa, the study

of the sugar content of nectars has been greatly simplified. In his earlier work Park collected nectar from the flowers, but after a long and thorough investigation of the sugar content of nectar in the honey-sacs of foraging bees, he has shown that no appreciable change takes place in the sugar concentration during the homeward flight, so that it is possible to determine the sugar concentration of nectar of a plant worked by the bees by observation on the contents of their honey-sacs. It will be evident that this method is far simpler than that of collecting microscopic amounts of nectar from a number of flowers, for example of white clover.

It is obvious that the amount of nectar secreted by different plants must vary enormously. *Protea mellifera* of South Africa secretes nectar in such abundance that it is collected by dipping a spoon into the flower, and nectar flows in long strings from *Eucalyptus ficifolia*; at the other extreme we have the most important honey plants of the world (the clovers) in which nectar occurs only in quantities which can be expressed in terms of milligrammes.

One of the most interesting investigations on the yield of nectar from a representative honey plant was carried out by G. E. Marvin on the tulip-tree (*Liriodendron tulipifera*) in the vicinity of Washington, D.C. In this district the tulip-tree blooms in the latter part of May, and in the height of the flow, if a gentle breeze is stirring the branches, the falling drops of nectar give the impression of a gentle rain. If the black locust (*Robinia Pseud-acacia*) is in bloom at the same time the bees neglect the abundance of nectar on the tulip-tree.

According to Marvin the numerous flowers of the tulip-tree resemble tulips and have six greenish-yellow petals arranged in two whorls to make a bell-shaped corolla. There is an orange-coloured strip, about 5 cm. wide, which forms a band around the cup about 15 mm. from the base. The nectaries are situated on the inner orange-coloured surface, as many small droplets of nectar collect there in freshly opened flowers; as the droplets increase in size they flow down and collect in the corolla of the flower. The nectar yields a reddish amber-coloured honey of good quality, but rather strong flavour.

Marvin adopted the method of covering with cellophane, each evening, the large buds which appeared ready for opening next morning. The blossoms were each labelled as they opened, so that their ages were known at all times. The cellophane was replaced after each collection of nectar. The weight of nectar in the flowers was determined by absorbing it in small pads of absorbent cotton which had been previously dried in an oven and stored in a desiccator. As required, a wad was withdrawn from the desiccator with a forceps and packed into the corolla of the flower, and the increase in weight due to the absorbed nectar determined. The nectar for the sugar determination was collected in a small glass pipette, the sugar was then estimated by means of an Abbe refractometer and Schonrock's tables. It was found that the average weight of nectar from a blossom was 1·6417 grammes, and the extremes were 3·1626 and 0·4748 grammes.

Nectar was found in the flowers during the first day and the following morning. If this nectar was removed, the blossom remained dry from that time onwards.

The average sugar content of the nectar in blossoms which had just opened was 16·7 per cent, but it increased to 21·1 per cent after the blossoms had been open for two hours and to 26·6 per cent after 4 hours. Blossoms which had been open since the previous day had a concentration of 36 per cent sugar in the partly evaporated nectar.

Observations were made on a tree which was 15½ inches in diameter at a height of five feet above the ground. The tree had 23 limbs and each limb carried, on an average, 108 blossoms, so that the total number of blossoms was 2484, as the average weight of nectar per blossom was 1·64 grammes the total weight of nectar was 4100 grammes, or 9·02 pounds. If we assume that the honey from this nectar, after ripening by the bees, contained 20 per cent water, its weight would be 2·16 pounds.

It is difficult to obtain a reliable figure for the average weight of a load of nectar carried by a bee, but it is of the order of 0·025 grammes. As a pound is approximately 450 grammes, it follows that 18,000 bee flights are necessary to carry a pound of nectar to the hive, hence about 72,000 bee-flights are necessary to collect sufficient nectar to make a pound of honey and a total of about 150,000 bee-flights would be necessary to collect all the nectar from the blossoms of the tulip tree. Obviously we have selected a tree which is particularly rich in nectar. In comparison, in the lime (*Tilia* spp.), regarded as a valuable source of nectar, the amount produced by a single blossom ranges from 2 to 3·5 milligrammes, but its sugar content is approximately 36 per cent. As regards the yields of nectar from some of the most important honey plants, a general impression of the amounts may be obtained by recalling that a bee visits 90 buckwheat florets in order to gather a load of honey ; that is, the weight of nectar per floret is of the order 0·0003 grammes ; from the sugar content of the nectar it can be calculated that the bee must visit 50 million buckwheat florets to obtain a pound of honey, and as a colony of bees often gather as much as 500 pounds per annum in a good buckwheat region the bees must visit 25,000 million florets in order to gather the nectar to produce this amount of honey—it should be realized that of this 500 pounds of honey only about 100 pounds is available as surplus to the bee-keeper, as the needs of the colony for its own existence is of the order of 400 pounds per annum. If the nectar in red clover plants were all available to bees sufficient could be gathered from five million florets to yield a pound of honey. It is hardly necessary to mention the significance of these figures, as evidence of the pollination values of bees.

The sugar content of nectars.

As already stated, the principal sugar present in nectar is sucrose, but glucose and laevulose are also found in the nectars of many plants. The sugar content of nectar determines the amount of honey which is obtained from a given weight of nectar ; hence it is an important factor in determining the value of a plant to the bees.

The classical papers on the composition of nectar are those of A. von Planta and of Gaston Bonnier. Before the development of modern micro-chemistry and the simple form of the refractometer, as many plants yield such small amounts of nectar from a single flower, the nectar was determined by making a water or alcohol extract of a definite number of flowers and estimating the sugar found in solution.

In certain flowers this method extracted some sugar from the floral tissues, so that the results obtained were not strictly accurate. The following results were obtained by von Planta by the use of the extraction method :—

Plant.	Sugar in nectar. per cent.
Protea mellifera	17·1
Hoya carnosa	40·6
Tecoma radicans	15·3
Fritillaria imperialis	6·6

These results indicate the total amount of sugar present and no attempt was made to determine the ratio of sucrose to glucose and laevulose. Bonnier attempted to differentiate between reducing and non-reducing sugars, as shown in the following table :—

Plant.	Water.	Sucrose.	Glucose.	Gums, ash, etc.
	%	%	%	%
Lonicera Periclymenum	76	12	9	3
Lavandula vera	80	8	7·5	4·5
Fritillaria imperialis	95	1	1·5	2·5

(The ' Glucose ' figures returned by Bonnier represent the reducing sugars : that is, glucose and laevulose as distinct from the non-reducing sugar sucrose.)

It is of interest to note that Bonnier states that bees pay no attention to the *Fritillaria* blossoms because of the extremely low sugar content in the nectar.

In his famous paper on ' Environmental Influences on Nectar Secretion ', L. A. Kenoyer (1916) carried out an important series of observations on the amount of nectar secreted by plants under various conditions of humidity, etc., and made estimations on the sugar concentration, but his results are too extensive to be summarized here. The paper, however, is a landmark in the study of nectar and should be read by all those seriously interested in the subject.

An elaborate series of experiments was carried out by Ruth Beutler, in Germany, on the composition of nectars, and her work probably marks the beginning of the scientific study of nectar. Some of her results are summarized in the following table :—

Plant.	Number of samples.	Glucose and laevulose.	Sucrose.	Total sugars.
	%	%	%	%
Plum	12	16·5	16·0	32·5
Paradise Apple	4	23·7	24·7	48·4
Fritillaria imperialis	9	9·4	—	10·1
Horse chestnut (*Aesculus*)	15	2·5	72·2	74·7
Thermopsis montana	8	20·4	29·8	50·2
Asclepias cornuti	18	2·0	25·9	27·9
Asclepias curassavica	3	1·7	18·6	20·3
Lonicera Caprifolium	11	5·8	20·4	26·2
Lonicera Heckrotti	14	5·1	17·5	22·6

The most important results shown in this table are the exceptionally high content of sugars in the nectar of the horse chestnut (at this concentration the solution is already supersaturated) and the marked variation in the ratio of reducing to non-reducing sugars as the ratio

is nearly unity in the plum and the apple nectars and only about 0·03 in horse chestnut nectar. All these nectars had a distinctly acid reaction, with the exception of the nectar from the plum, which was alkaline.

The most comprehensive list of analyses of sugar in nectar has been given by Vansell, and a selection of his results is given in the following table :—

Name of plant.	Percentage of sugar in nectar.
Red Filaree (*Erodium cicutarium*)	65·0
Black Locust (*Robinia pseud-acacia*)	63·2
Willows (*Salix* spp.)	60·0
Astragalus pachypus	59·2
Wild Buckwheat (*Eriogonum* sp.)	58·1
Saintoin (*Onobrychis sativa*)	55·4
Big-leaf Maple (*Acer macrophyllum*)	52·0
Wild Alfalfa (*Lotus glaber*)	52·0
Yellow Sweet Clover (*Melilotus officinalis*)	51·6
Dandelion (*Taraxacum officinale*)	51·2
Mustard (*Brassica* spp.)	50·5
Apples, several races	50·0
Chickweed (*Stellaria media*)	50·0
Cherry, Sweet	50·0
Flax (*Linum usitatissimum*)	49·5
Horehound (*Marrubium vulgare*)	48·3
White Sage (*Salvia apiana*)	48·0
Crimson Clover (*Trifolium incarnatum*)	47·7
Black Sage (*Salvia mellifera*)	44·9
Alsike Clover (*Trifolium hybridum*)	43·3
Alfalfa (*Medicago sativa*)	41·1
White Clover (*Trifolium repens*)	41·0
Spikeweed (*Centromadia pungens*)	39·9
Yellow Star Thistle (*Centaurea solstitialis*)	37·5
Milkweed (*Asclepias* sp.)	37·2
White Sweet Clover (*Melilotus alba*)	35·8
Evergreen Blackberry (*Rubus vitifolius*)	35·6
American Linden (*Tilia americana*)	33·6
Creeping Sage (*Salvia sonomensis*)	32·4
Navel Orange (*Citrus sinensis*)	30·0
Peaches (*Persica vulgaris*)	30·0
Blue Curls (*Trichostema lanceolatum*)	27·1
Turkey Mullein (*Eremocarpus setigerus*)	25·0
Tulip Poplar (*Liriodendron* sp.)	19·6
Avocado (*Persea gratissima*)	15·2
Apricots	12·0
Madrone (*Arbutus Menziesii*)	10·0

In addition to the observations on floral nectar, Vansell made a series of most interesting determinations on the sugar content of nectars from extra-floral nectaries in various species of vetch, and his results are shown in the following table :—

Kind of vetch.	Source of nectar.	Percentage of sugar.
Common	Blossom	22·6
	Stipular	56·5
Hairy	Blossom	44·0
Hungarian	Blossom	25·2
	Stipular	47·7
Melanops	Blossom	22·6
	Stipular	52·1
Purple	Blossom	28·0
Wild	Blossom	23·1

These records are the average of numerous readings and were taken during various times of day, so that they are truly representative of the sugar content of the nectars from the two different sources. It will be observed that in each case the sugar content of the extra-floral nectaries is nearly twice the value of that from the floral nectaries. Vansell emphasizes the fact that honey-bees confined their attention almost exclusively to the extra-floral nectaries and disregarded the nectar from the blossoms when both sources were yielding nectar.

The catalpa tree, which grows in abundance in Kansas, has extra-floral as well as floral nectaries, and honey-bees have often been observed busily gathering nectar from the extra-floral nectaries when none were working on the floral nectaries.

The cotton plant has three sources of nectar, namely, the floral, the involucral and the leaf gland nectaries. Observations on Acala cotton kept in a humid atmosphere showed that the involucral nectar contained 17 to 24 per cent of sugar, the leaf gland nectar 12 per cent, but the floral nectar contained only 7 per cent.

The partridge pea (*Cassia chamaecrista*) is entirely devoid of any floral nectar, but nectar is secreted by an extra-floral gland located on the upper side of the petioles. The gland is saucer-shaped and nectar may be gathered continuously for three months or more, and in some of the dry sandy regions of Georgia the plant is the main source of surplus honey.

It is very difficult to understand why a plant should secrete extra-floral nectar of higher sugar content than that of the floral nectar, and thus reduce the activities of the honey-bee in fulfilling its purpose in pollinating the flowers. It is not easy to reconcile the teleological argument for nectar secretion with the existence of the higher sugar content of extra-floral nectar.

The concentration of sugar in nectar plays a very important part in the selection of flowers which are worked by the honey-bee in a neighbourhood where a variety of plants are secreting nectar at the same time. It has already been mentioned that the bees sometimes neglect the copious flow of nectar from the tulip poplar and devote their attention almost exclusively to black locust trees in the same locality. It is fairly reasonable to conclude that they find the nectar of 63 per cent sugar concentration from the black locust much more attractive than the nectar from the tulip poplar at about 20 per cent sugar concentration. In support of this theory some further results obtained by Vansell during his work on the nectar of several races of plum, at Davis, California, are most convincing. The different races of plums grew side by side in the same orchard.

Race of plum.	Percentage of sugar in nectar.	Number of blossoms required for sample
Maynard	10·1	8
Gee Whiz	13·5	12
Eldorado	14·9	15
Miss Edith	16·1	18
Shiro	17·8	12
Etta	19·0	15
First	23·3	15
Milton	28·4	20
Kelsey	—	—
Better than Gold	—	—
Kingdom Come	—	—

In the last three races the nectar was insufficient for collection by hand, and the bees were entirely absent from blossoms. The race Milton was outstanding in the number of bee visitors, as the bees were lured to the blossoms containing the highest sugar content and paid no attention to the blossoms secreting nectar of low sugar content *. If the production of richer nectars is a hereditary characteristic we have a basis for the selection and breeding of better honey plants or races of fruit trees with superior pollination qualities.

Vansell's tables show that there are wide variations in the sugar content of nectars ranging from 4 per cent in certain pears to 65 per cent in red filaree (*Erodium cicutarium*). Perhaps the highest sugar content is shown in the nectar of *Origanum vulgare*, which contains 76 per cent, as described in a paper of particular interest by Miss Elizabeth Kleber. Scullen and Vansell find that the grape (*Vitis* spp.), in Oregon, secretes nectar with a sugar content ranging from 65 to 75 per cent. The same authors investigated the influence of relative humidity on the sugar content of the nectar of fireweed (*Epilobium angustifolium*) in which the nectaries are much exposed, and therefore highly susceptible to variations in atmospheric conditions :—

Relative humidity.	Percentage of sugar in nectar.
79	19·00
75	27·10
70	36·78
65	38·41
60	37·31
55	47·15
50	49·80
45	58·69
40	61·20
35	64·93
30	65·66

The influence of relative humidity depends on the structure of the blossom ; that is, whether they are of the open or tubular type. Thus nectar in a tobacco blossom, which is of the tubular type, shows but little change, and even on a warm dry day seldom exceeds 25 per cent in sugar content, whereas in a plum blossom, which is of the open type, the nectar in the race Milton is rapidly concentrated to 40 per cent sugar content.

In general it has been found that nectar is secreted most abundantly during periods of high humidity, and as long ago as 1878 Gaston Bonnier stated that the quantity of nectar secreted varied directly with the relative humidity. Hugo Haupt showed that although flowers of buckwheat (*Fagopyrum esculentum*) and touch-me-not (*Impatiens Sultani*) kept under experimental conditions in air of 100 per cent relative humidity secreted a greater volume of nectar than did the same plants

* Butler has pointed out that it is important to eradicate weeds, etc., from orchards as these may yield nectar of higher sugar content than the nectar secreted by the fruit trees. I have found, for example, that dandelion nectar contains 38 to 46 per cent sugar.

exposed to a drier atmosphere, the total amount of sugar was not thereby increased. Kenoyer showed that the nectar of touch-me-not in a saturated atmosphere contained 23·4 per cent of sugar, but in the drier atmosphere of a greenhouse the same plant yielded nectar of 45·3 per cent sugar content. It is evident, therefore, that increase in volume of nectar secreted is not necessarily an advantage for the production of honey.

O. W. Park studied the sugar content of flowers with exposed nectaries, such as basswood (*Tilia americana*) and the common milkweed (*Asclepias syriaca*), and found that the sugar concentration varied inversely with the relative humidity. He also found that the effect of humidity was much more pronounced on the nectar of the 'open' flowers than upon that of the well-protected nectar in the blossoms of trumpet creeper (*Tecoma radicans*), gladiolus, day lily (*Hemerocallis*) and Canna.

The increase in quantity of nectar under humid conditions may therefore, be regarded as a disadvantage for two reasons. In the first place, the more dilute nectar involves the concentration of a greater quantity to produce a pound of honey, and in the second place the lower concentration of sugar reduces the incentive to gather the nectar. During periods of high humidity the nectar of the orange blossom, for example, is secreted at a sugar content of 16 per cent and the bees almost ignore the abundant supplies of orange nectar for the more concentrated nectars of mustard (*Brassica campestris*), wild radish (*Raphanus sativus*) and horehound (*Marrubium vulgare*), which secrete nectar of 45 per cent sugar content or more. When the humidity decreases the orange nectar is concentrated and the sugar content soon reaches a value of 55 per cent, so that the bees now cluster on the orange blossoms and ignore the other flowers.

As so much emphasis has been placed upon the importance of the sugar content of nectars, it is of interest to mention some observations by von Fritsch on the sense of taste in bees. It was found that the liminal concentration of sucrose solutions acceptable to bees depends on their degree of hunger; normally the concentration is about 17 per cent, but the threshold value is probably between 4 and 8 per cent. For glucose the normal value is 18 per cent, and it has been established that the effect of various mixtures of different sugars is additive. The sugars glucose, fructose, maltose, trehalose, and melezitose are acceptable to bees, but their sense of 'sweetness' is more limited than in man, as they show no interest in dulcin, saccharine, glucine, eupatorin or glycyrrhizic acid. As the sugar content of the nectars of avocado, apricots, sour cherries and certain pears is less than 17 per cent, it therefore follows that bees will pay little attention to the blossoms of these fruit trees if more attractive nectars are available.

Factors which influence nectar flow.

The flow of nectar is the most fundamental factor in honey production, but the conditions which determine the amount of flow appear to be due to the integrated effects of a great number of independent factors concerning which we possess very little precise knowledge at the present time. Variations of nectar flow present a problem of great interest to

the naturalist and are of supreme importance to the bee-keeper. It may be assumed that the nectar flow of any particular plant depends upon the weather conditions during the period of flow ; the weather conditions during the previous autumn, winter and spring and possibly still earlier ; the soil ; the latitude and the altitude at which the plant is growing. Individual species of plants vary enormously in the amount of nectar which they normally secrete ; they also vary in the time of day during which their nectaries are active, thus buckwheat secretes nectar in the morning only, red maids (*Calandrinia caulescens*) from noon to dusk only and certain Australian Eucalypti during moonlight nights as well as during the day. It has been shown, however, that the old belief that secretion is at its maximum during the period of full moon is not true. Most plants show a peak in their daily rate of flow, and Bonnier expressed the opinion that plants secrete the minimum quantity of nectar around noon.

Unfortunately, very little systematic work has been done on the correlation between the actual weight of nectar secreted by plants and the prevailing weather conditions, so that most of our impressions of the variations in nectar flow have been gleaned from observations on the gains in weight in colonies during the flowering period of nectar plants. These data, however, do not give a true indication of the variations in nectar flow, because the changes in colony weight are determined by two factors operating at the same time and both influenced by weather conditions. These factors are the influence of weather upon the plant and the influence of weather upon the activities of the bees. The position has been admirably summarized by Hambleton in the following passage :—

' It is quite evident that the factors influencing nectar secretion are not necessarily synonymous with those affecting the changes in weight of a colony of bees during the honey flow. . . . . If climatic conditions affect the behaviour of bees in the same manner as they affect nectar secretion, one would expect to find close correlation between factors reputed to be favourable both to nectar secretion and to increase in weight in the colonies of bees, but such a correlation does not seem to exist. It seems, therefore, that either the proper combination of factors influencing nectar secretion has not been discovered, or that the effect of weather conditions upon the behaviour of bees is entirely different from their effect on plants.

' It has previously been impossible to determine by judging from the changes in the weight of a colony of bees whether weather conditions influence the more greatly bee behaviour or nectar secretion ; and from the standpoint of the practical bee-keeper the influence of weather on colony weight is far more important than its influence upon either nectar secretion or bee behaviour alone '.

Before discussing the influence of weather and other factors upon nectar flow it is advisable to refer, briefly, to some of the chief characteristics of nectar flow and to the process of nectar secretion—in so far as it is at present understood. Perhaps the most important feature of nectar flow is the variation in the amounts produced from season to season. Ling or heather (*Calluna vulgaris*) is one of the most erratic plants in this respect, and the surplus honey gathered from a heather

moor varies enormously from year to year—although the weather may be ideal during the time of flow. Some of the best yields are obtained following a month of heavy rainfall in July, and some record daily yields have been obtained during days with heavy frost in the morning. Acres of white clover, in full flower in the height of summer, occasionally yield very little honey, and prosperous colonies have been known to lose weight during such periods. In Oregon the rose yields a surplus of excellent honey in certain seasons, perhaps once in three or five years, and the same is true of the vining milkweed (*Gonolobus laevis*) in Indiana.

It will be realized that it is extremely difficult, even with the aid of statistical analysis, to express the relationship between nectar flow and any of the weather factors, for example temperature, as it is almost impossible to vary one of the factors independently. A change in atmospheric temperature, generally, involves a change in relative humidity which, in itself, influences the amount of nectar flow. Bonnier expressed his opinion that the amount of nectar secreted varies inversely with the temperature, but Hambleton analysed his limited data and showed that for constant relative humidity nectar secretion varies directly with temperature. Kenoyer found that for most of the Leguminosae there was an optimum temperature of 59° F. for nectar secretion. He called attention to the fact that the storage of sugar in the twigs of woody plants increases with lowering of temperature and showed that the same is true for floral tissue. He further showed that the permeability of the nectar cells increases with temperature, and he concluded that the rate of secretion is determined by the opposing effects of these two factors; hence there must exist an optimum temperature for secretion, and this is the point of intersection of the two graphs showing the relationship between temperature and sugar storage, and temperature and permeability. It is probable that the temperature of 59° given by Kenoyer is too low and that the optimum temperature is nearer 63° or 65° F. Phillips and Demuth consider that secretion is at a maximum when there is a considerable daily range of temperature, and that the best results are obtained when the night temperature is below 65° F. and the day temperature well above that figure. There is an old belief amongst bee-keepers, as well as amongst certain scientific men, that 'Cool nights followed by warm days' are the ideal condition for nectar secretion. Wedmore states that: 'Probably a day temperature of about 80° F. with cool nights after a rainy spell gives the highest takings', but this statement naturally includes the factor of bee activity. The literature of bee-keeping abounds in references to the beneficial effects of high temperature on nectar secretion; on the other hand, there are indications that low temperatures play an important part in nectar flow. Wilson found that the rate of flow was hardly influenced by temperature; but in the case of *Prunus Laurocerasus* he observed that a minimum of 53° F. was necessary for the metamorphosis of the cell walls and the raising of the cuticle, but afterwards a much lower temperature enabled secretion to continue. Haupt considered that a minimum temperature was necessary and Demuth observed that basswood (*Tilia americana*) did not produce nectar below 64° F. in Indiana. It will be agreed that a great deal more systematic work is necessary before the influence of temperature on nectar secretion is clearly understood.

As sunshine exerts such an important influence on plant life it is natural that a great many experiments have been designed to determine its effect on nectar secretion. We will confine our remarks to a few of the more interesting results, some of the earliest of which were obtained by Ono, who showed that the young extra-floral nectaries of *Ligustrum lucidum*, *Viburnum japonicum*, *V. Opulus*, *Prunus yedoensis* and *P. Laurocerasus* produced no nectar at all in a dark, moist chamber, but that their fully-developed nectaries secreted just as freely in the dark as in sunshine. *P. Laurocerasus* continued to secrete nectar in abundance for three weeks in a dark chamber, even though the nectaries were washed daily. Ono came to the conclusion that secretion may occur by mere chance and that the internal condition of the nectary was of far greater importance than the external factors, provided that they are favourable to the life and growth of the plant. On the other hand, Haupt found that for *Euphorbia* and *Vicia* nectar secretion is greatly influenced by light, and especially by the red and yellow light of the sun's spectrum; that secretion of nectar occurs only in light; and in darkness or in blue light nectaries already containing sugar resorb this substance. Wilson does not believe that light plays an important part in nectar secretion, because he observed that many plants secrete just as freely in darkness as in sunshine, while others require either direct or diffused sunshine to stimulate secretion. On the other hand, Livingston expressed his opinion that light is the most important of all external factors on plant transpiration. It would be a subject of great interest to correlate the amount of nectar flow with length of day, as this factor, as shown by Garner and Allard, has such a profound influence on the growth and flowering of plants.

Lastly, we may refer briefly to the effects of relative humidity, as certain species of plants secrete nectar freely under conditions approaching saturation with moisture, whereas others secrete nectar in arid or semi-arid localities. It is important to bear in mind that relative humidity influences the sugar content of nectar, so that in order to obtain a true estimate of secretion it is necessary to determine not only the volume of nectar, but the sugar concentration as well, so that some of the following remarks cannot be regarded as of much value as evidence. Both Hommell and Ono state that nectar secretion increases with increasing relative humidity, and the latter adds that a dry atmosphere is unfavourable to secretion. Ono placed some cut twigs of *Prunus Laurocerasus* in a vessel of water under a bell jar, and they continued to secrete nectar at a constant rate and of constant sugar content for three weeks, although the nectaries were washed daily. Wilson found that a branch of a plant of the same species continued to secrete nectar in a dry room until the branch had lost over a fourth of its weight. It was necessary to stimulate secretion before the beginning of the experiment by keeping the plant in a moist atmosphere in a bell jar. It is interesting to recall that Vines states that 'the structure of a nectary is essentially similar to a water gland, but its properties are very different. We have seen that the excretion of liquid by a water gland is entirely dependent upon the root pressure: when the organ bearing the water gland is separated from the rest of the plant, the secretion at once ceases. It is not so with a nectary. If a flower containing nectaries, that of *Fritillaria*

imperialis for example, be cut off and the drops of nectar be removed by means of blotting paper, it will be found, after a time, that large drops have been excreted. The cells of the nectar, like the parenchymatous tissue of the root, have the power of setting up within themselves so great a hydrostatic pressure as to force out by filtration the liquid which they contain'. Kenoyer found that by increasing the relative humidity the total amount of nectar was increased, but not the amount of sugar. Here, again, it is evident that further work is necessary before we can make any definite statement regarding the influence of relative humidity upon secretion.

As regards the mechanism of secretion, it is very difficult to obtain authoritative expressions of opinion, and few botanists seem to be in a position to discuss all the factors involved in the process. A distinguished botanist has, however, informed me that 'nectar secretion is considered an osmotic phenomenon. The membranes of nectaries are semi-permeable and permit the passage of a certain amount of sugar. At the exterior of the nectary the sugar solution loses water by evaporation and the stronger solution then exerts an osmotic effect in causing some solution to pass out of the cell. If the sugar solution (or crystallized sugar) is removed completely from the exterior by washing, or other means, the secretion stops'. This statement gives a very simple explanation of the process, but it can hardly be accepted as complete; for instance, it does not explain why nectar begins to flow, and assumes that continuity of flow depends upon evaporation, although, for example, in the experiments of Ono quoted above, no evaporation could take place. It is possible that secretion begins according to the theory of Pfeffer, that the outer portion of the cell wall is transformed into sugar and thus initiates the osmotic effect upon the contents of the cell. This is supported, to some extent, by Wilson, who found that thorough washing of the nectary stops the secretion if the nectary has passed the stage of metamorphosis of the cell wall, but that secretion is resumed on the addition of sugar to the external surface of the nectary. It is evident that the nectary resembles a semi-permeable membrane, or a diffusion membrane, as it readily permits all compounds of low molecular weights to diffuse through, as is shown by the fact that nectar contains all the soluble salts present in cell sap as well as sugars and other simple organic compounds, but proteins are 'filtered out', as they are not usually present in nectar to any appreciable extent.

As far as I am aware, no complete theory has been evolved of the mechanism of nectar secretion, but it is probable that a thorough investigation of all known facts in the light of physical chemistry and plant physiology would lead to a satisfactory explanation. For the present, therefore, we must assume that no theory can explain the diffusion of a dilute solution of sugar into a more concentrated solution of nectar; for example, in the maple, where the sap contains only 2 per cent of sugar and the nectar 60 per cent or more.

Influence of weather during time of flow.

The quotation from Hambleton's paper shows that it is not possible to separate the influence of weather upon the activities of bees from

the influence of weather upon nectar flow by means of observations in changes of hive weights during flow. Nevertheless, it is of interest to describe some observations made on colony weights during the time of flow and correlate them with the weather in general, and also with the various factors, such as temperature, sunshine, etc., involved in the study of the weather. An excellent example of the study of the effect of weather, as a whole, over a period of eleven years was made by Krishnamurti at Rothamsted. The observations were confined to the months of May, June and July, as these are the three most important months for nectar flow in the south of England. The following table gives the net gains in weight of the same colony of bees, and it will be evident that the fluctuations from year to year are very pronounced :—

Monthly and total gross gains, in pounds at one hive during May–July, 1928–1938.

Year.	May.	June.	July.	Total.
1928	12	53	83	148
1929	39	78	26	143
1930	5	21	24	50
1931	0	24	18	42
1932	5	53	13	71
1933	23	19	69	111
1934	16	31	41	88
1935	3	20	91	114
1936	30	18	2	50
1937	3	14	39	56
1938	0	13	14	27

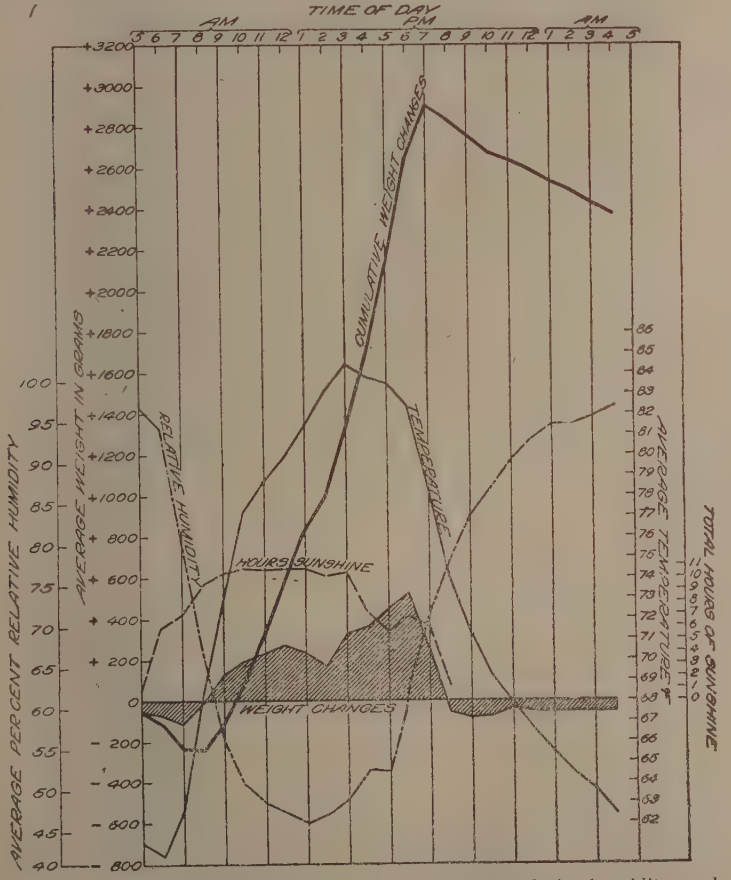
Krishnamurti did not attempt to make a complete statistical analysis of the relationship between gains in weight and the various weather factors during the period of nectar flow, but he was able to show that high temperatures, long hours of sunshine and rainfall below the average are desirable for successful honey production. The years 1928, 1929, 1933 and 1935 are good years, 1932 and 1934 are moderate, and the rest are poor. From an analysis of the weather conditions it was shown that years of favourable weather conditions are succeeded more or less regularly by unfavourable ones. This appears to confirm the conclusion of E. G. Burtt that in England three good honey years were followed by three bad ones during the seven-year period 1932–1938. This conclusion also holds good for the period 1928–1932. The years 1928, and 1929—two good years—are followed by two poor years and one moderate year. In the south of England, therefore, between 1928 and 1938 there appears to have been an alternate series of short groups of good and poor years for honey production.

Kenoyer analysed the results obtained during observations extending over 29 years in an apiary in Iowa, and concluded that a good honey crop tends to be preceded and followed by a poor one ' very much as is known to be the case with the apple crop ', and added that ' evidently there is in a year of heavy yield exhaustion of the honey plants from which they do not quite recover in the following year '. He summarized his observations in the following convincing form :—

Relation of good and poor production years.

Average for year preceding ten best years	74·6 lbs.
Average for year following ten best years	71·9 „
Average for year preceding ten poorest years.....	136·5 „
Average for year following ten poorest years	126·3 „

Hambleton's paper, already mentioned, is a landmark in the development of the study of the influence of weather during the period of flow



Graph of average hourly weight changes, temperature, relative humidity, and total hours of sunshine. (Hambleton.)

upon the gain in weight of a colony of bees. He made a very thorough statistical analysis of the various weather factors concerned with honey production, and introduced the idea of hourly, rather than daily, readings

of the change in weight of a colony, and thus obtained a much more accurate picture of the fluctuations in weight and their relationship to the various factors influencing nectar flow and bee activities. Only a very brief summary of his methods and results can be given here, but the original paper deserves serious study. The daily observations made on one hive is shown in the graph above, and it is important to realize that the shaded curve shows the variations in weight from hour to hour, and the additive effect of these hourly gains (or losses) are shown by the solid line described as 'Cumulative Weight Changes'. Curves are also included for the weather factors, temperature, relative humidity and hours of sunshine.

One of the most impressive features in the diagram is the 'midday decline', which is the name given to the decline in the amount of gain from hour to hour occurring near midday. Although gains actually take place during this period on most days, there is a noticeable difference in the rate of gain at this time compared with that of the hours immediately before and after, and it can be shown that the midday decline reduces the yield of honey by as much as 15 or 16 per cent. Bonnier measured the amount of nectar produced at various times of the day and found that less nectar is produced towards the middle of the day. He also found that at this time bees return to the hives with less than their maximum loads, and that fewer bees leave the hive during this period in comparison with periods before and after. The reasons for these changes on the part of the bees and the flowers are not yet understood.

Hambleton summarized his results in terms of correlation coefficients, expressing the relationship between gain in weight and the various weather factors, but found it necessary to classify his results into two groups, referring to spring and autumn periods, as shown in the following table :—

Weather factor.	Correlation coefficients. Spring period.	Autumn period.
Average temperature	75·29	−23·10
Hours of sunshine	61·24	5·95
Temperature variation	59·67	55·70
Solar radiation	55·25	−3·41
Variation in relative humidity	42·29	53·91
Average relative humidity	−12·64	−9·60
Unknown factors	34·70	53·60

(The probable error was not significant in any of the results.)

The two columns are not strictly comparable, as in the spring period only days which showed a minimum net gain in weight of 980 grammes were considered. Although Hambleton emphasizes that the factors which influence the secretion of nectar do not similarly influence change in colony weight, one cannot avoid being impressed by the high degree of correlation in the first four weather elements and change in colony weight in the spring period, and wish that a thorough investigation could be made of the influence of weather factors on actual nectar flow, and preferably in terms of the amount of sugar secreted in a definite period by the plant.

The influence of past weather on nectar flow.

In an attempt to estimate the effect of past weather upon nectar flow one has to adopt the method of correlating the amount of honey obtained from a colony with the past weather. It is obvious that such a method is by no means satisfactory, as the surplus honey obtained depends to a great extent upon the condition of the bees—a condition determined by the weather during the preceding winter and spring. Nevertheless, it is of interest to recall some observations made by Kenoyer, who concluded that a cold winter was not detrimental to the yield of honey in the following summer. A warm March, however, appears to precede every good honey season, but he states that this may be due partly to the better development of the colony and the greater vigour of the plants. The results for winter snowfall were definitely in favour of those years which showed excessive fall; of the winters preceding the ten best seasons in Iowa, over a period of 29 years, the average snowfall exceeded that of the winters preceding the ten poorest years by 16·5 inches. The advantage is probably due to the increase in moisture available to the plants and the protection given to the clovers.

Kenoyer also stated that abundant rain seems essential to stimulate plants to yield a good nectar flow, and the following table shows that the best honey years follow seasons in which the rainfall has been above the normal. Each period listed shows a greater rainfall for the ten best years than in the ten poorest years, especially the month of May. As June is the month in which nearly 60 per cent of the nectar is gathered in Iowa it is evident that a low rainfall is an advantage for the activities of the bees during this period.

Rainfall in good and poor years of honey production.

	Average for 10 best years.	Average for 10 poorest years.
	inches	inches
Rain for year	33·49	30·32
Rain for preceding year	35·09	30·39
Rain for preceding July to September	11·75	10·12
Rain for preceding October to December	6·63	4·71
Rain for preceding January to March	3·97	3·64
Rain for April	2·99	2·59
Rain for May	6·51	3·02
Rain for June	4·07	4·87

The above data are of particular interest in the light of a very promising theory regarding the influence of past weather upon annual variations in nectar flow due to R. G. MacLachlan, an Australian editor and bee-keeper. Most of the observations, extending over thirty years, refer to Australian honey-plants, and in particular to eucalyptus trees, which are a very important source of nectars. MacLachlan postulates that nectar secretion is a process designed to maintain the constant composition of cell sap, especially the carbohydrate-nitrogen ratio. He regards the nectary as a 'filter', or a diffusion membrane, which permits the flow of water, sugar, metallic salts, etc., but retains nitrogenous compounds, such as proteins; he emphasizes that the most important

qualitative difference between cell sap and nectar is the absence of nitrogen, in general, in the latter. There are also quantitative differences in the proportions of water, sugar, metallic salts, etc., and these arise from the selective permeability of the membrane. He states that the carbohydrate-nitrogen ratio varies during the life of the plant, which may be divided into two different periods—the period of growth and the period of bloom and reproduction. During growth the plant stores carbohydrate as starch, but during bloom the starch is converted into sugar and carried by the sap to the flowers. A portion of the sugar is used in the formation of flowers and seeds, and a portion is secreted as nectar, and he maintains that the extent of these two portions is determined by the carbohydrate-nitrogen ratio at the time of bloom. As nitrogen is an important component of flowers and seed, the amount of sugar necessary depends on the nitrogen available for this purpose. If, therefore, the carbohydrate-nitrogen ratio is in excess of that required to form flowers and seed, the excess sugar will be secreted as nectar and the flow will increase with increasing value of the excess ratio ; but if the carbohydrate-nitrogen ratio does not exceed that required to form flowers and seed, then no nectar will be secreted. On this theory, therefore, any factor which tends to increase the carbohydrate-nitrogen ratio will lead to increase in nectar flow.

MacLachlan states that it is not the day-to-day activities of the plant in carbon assimilation which determine the carbohydrate-nitrogen ratio at the time of bloom, but the integrated effects of the plant's experience since the last period of bloom. He cites, as an example, a grove of red gums (*Eucalyptus rostrata*) which gave an abundant flow of nectar, although the trees were leafless during bloom and had been for some time, owing to a plague of insects. *E. elaeophora* blooms biennially and *Leptospermum scoparium* annually, but they produce a nectar flow only once in six years or more, and this he ascribes to the weather since the previous flow. It is essential for the plant to pass through a period of vigorous growth, accompanied by the development of abundant foliage since the previous flow in order to synthesize and store the necessary carbohydrate before the following nectar flow, and it must therefore be supplied with sufficient rainfall or moisture to induce active growth. If the amount of moisture available between two consecutive blooms is not sufficient to yield a nectar flow, the carbohydrates, according to MacLachlan, can be ' banked up ' until the following nectar flow. If, however, there is heavy rainfall during, or immediately preceding, bloom, the plants continue to grow, and, therefore, absorb nitrogen from the soil ; as both carbohydrate and nitrogen are required for growth, the excess of the former required to produce a nectar flow is reduced, so that secretion is at a minimum. In general, any factor, such as thunderstorms, which checks growth, leads to nectar secretion ; and any factor which induces growth, such as abundance of moisture, leads to a decrease of nectar secretion.

The above brief résumé of MacLachlan's theory does not give a complete picture of his ideas and of the wealth of observational evidence he has collected in its support. The theory deserves serious attention by botanists and bio-chemists, and a great deal of work remains to be done

on the differences in composition between cell sap and nectar in a plant, as a complete analysis of these materials for a large number of species of trees and flowers will enable us to determine, with some degree of precision, the nature of the processes underlying the flow of nectar.

Influence of soil on nectar secretion.

Hardly any experimental evidence of the influence of soil upon nectar secretion is available; there is a good deal of indirect evidence based upon the yield of surplus honey obtained from the same species of plant grown in different types of soil. As far as is known, soil conditions do not directly affect nectar secretion, but only indirectly, through their effects upon the general well-being of the plant. It is generally agreed that vigorous plants yield more nectar than do those in an undeveloped state.

Plants appear to yield most nectar when grown under the most favourable conditions. Sainfoin, an important plant in the Cotswold region, secretes most nectar when grown on a limestone subsoil. White clover is regarded as an important honey plant wherever there is abundance of lime in the soil; if there is a deficiency of lime the plants secrete nectar only under the most favourable climatic conditions. Sourwood (*Oxydendron arboreum*) and heather (*Calluna vulgaris*) yield only on slightly acid soils rich in humus, and willow herb (*Epilobium angustifolium*) grows abundantly on rocky soils following a fire. Black mangrove (*Avicennia nitida*) has been known to give a surplus of 400 pounds of honey when growing in Florida soils containing over one per cent of salt.

Buckwheat, which is grown extensively as a farm crop in New York State, Ontario and the surrounding country in light sandy soils of slight acidity, gives heavy yields of nectar and surplus honey each year. Bee-keepers assumed that it would grow equally well in Iowa and in the Middle West, and planted extensive areas of buckwheat in these region; but a surplus of honey is hardly ever obtained.

Cotton yields nectar freely where the soil is rich and heavy; but in neighbouring areas where the soil is light and sandy very little honey is obtained, although cotton plants are equally abundant.

Goldenrod (*Solidago*) is one of the most important honey plants in New England, but in the Mississippi valley, where it grows in profusion, it is seldom of any value to bees. Alfalfa contributes no honey east of the Mississippi, but it is an important plant further west.

The influence of fertilizers upon nectar secretion has not yet been determined; neither is anything known, with certainty, of the effects of the relative proportions of available phosphorus, nitrogen and potassium in the soil. MacLachlan states that soils suitable for fruit and root crops are also suitable for honey. He states that in one area in Victoria the soil is deficient in potassium, and it is the only area in the State where potato yields are increased by potassium fertilizers. It is also the area in the State where honey production is at a minimum. Further east there is excellent honey country and yields are abundant, both from eucalyptus trees and from clovers, and the soil is found to be rich in potassium. MacLachlan adds that the honey-producing areas of the State are characterized by abundance of potassium in the soil,

though many of them are naturally poor in nitrogen and phosphorus. On the other hand, Sistek maintains that the development of nectaries is conditioned by the presence of nitrogen, but their activities by the presence of phosphorus. He found that on light soil, poor in nitrogen but manured with phosphorus, white clover was eagerly worked by bees and yielded much seed, Swedish clover (*Trifolium hybridum*) grows best in wet soil, but the formation of seed is largely determined by the amount of phosphorus present.

Recently Lundegardh has developed the method of leaf analysis as a criterion of the availability of nitrogen, potassium, phosphorus and calcium in the soil. It is probable that this idea could be usefully extended to correlate the nectar flow with the amounts of nutrient elements available to the plant as distinct from the amounts actually present in the soil.

Soil moisture also plays an important part in nectar secretion, but we do not know the relative effects of abundance of moisture during the growing and during the blooming periods: goldenrod yields most abundantly in New England after a wet summer followed by a dry autumn, but limes are stated to yield more freely when supplied with plenty of moisture at all periods, and secretion is at a maximum when the trees grow near water.

It would appear, therefore, that plants yield most nectar when growing in their natural habitat, but that we know very little of the influence of soil reaction or of fertilizers upon secretion. Much work remains to be done on this most important aspect of nectar secretion in different species of plants.

Influence of altitude and latitude on nectar secretion.

There exists a general impression that both high altitudes and high latitudes favour nectar secretion. It will be readily seen that it is very difficult to verify such a belief, as any change in altitude or latitude implies a change in soil, so that it would be necessary to conduct small-scale experiments under carefully controlled conditions, with the same soils, at different altitudes and different latitudes. So far the evidence rests upon general observations on the yield of nectar in a few plants growing naturally at different altitudes, and on the yield of honey from the same species of plant in different latitudes. Hermann Mueller found that the spur of an orchid (*Platanthera solstitialis*) was only about one-third full of nectar in the lowlands, but it contained 50 per cent more nectar in the Alps, and Bonnier stated that *Silene inflata* was much richer in nectar at a height of nearly 6,000 feet than at 1,300 feet; as far as we are aware no observations were made on the relative humidity, the sugar content of the nectar or of the type of soil at the different heights. Bonnier, also reports that the surplus yield of honey from a colony at the foot of the Pyrenees was only 6½ pounds, but at an altitude of 4,000 to 5,000 feet the yield was nearly twenty pounds of honey. One does not question these facts, but we do not think they are very convincing evidence in support of the influence of altitude on nectar secretion. On the other hand, much has been written in support of this belief and, in general, we are inclined to agree with the theoretical arguments

produced in its favour. It is claimed that as light intensity increases with altitude, and that there exists greater differences between night and day temperatures, both these factors must lead to increased secretion. The general conditions result in the dwarfing of the plants, and this is claimed to favour the growth of more and larger flowers and a more ample yield of nectar.

It is usually maintained in Britain that altitude favours the growth and secretion of heather, and that good heather honey is not obtained below the 1,000 feet level. It is true that, in general, the best heather honey is obtained from altitudes above this figure, but this is largely, and perhaps entirely, due to the absence of other plants in these areas, so that the observations really concern purity of sample rather than quality of nectar secreted by the heather. It should be borne in mind that we have examined heather honey grown in Dorset at a level of about 50 feet which was superior to many samples gathered above the 1,000 feet level in other parts of Britain. For the present we can safely say that we have no evidence that high altitudes improve the yield or quality of heather nectar; until we can find two areas with identical soil characteristics at differing altitudes the effect of altitude must remain an open question.

It has been found in California that sages yield much more honey at high altitudes than in the valleys, and the local writers on bee-keeping invariably express their belief in the favourable effects of altitude on nectar secretion. It is generally accepted that alfalfa is a good honey plant above the 1,000 feet level in eastern Kansas, but is inferior at lower levels. In the Imperial Valley, California, 200 feet below the level of the sea, it secretes nectar freely! E. F. Phillips states that near Washington tulip poplar grown above the fall-line gives a surplus regularly, but below the fall-line in the same neighbourhood a yield of honey is never obtained from this plant.

It is not possible to make any definite statement regarding the influence of altitude on nectar secretion, but most bee-keepers, and some scientists, are of opinion that increase in altitude favours honey production.

Surplus honey is obtained in all latitudes from the equator as far north as the province of Trondelag, in Norway, where the bees are actively engaged in gathering nectar till ten in the evening in the height of summer. It is believed that, within limits, the amounts of surplus honey increases with increasing latitude; but this does not necessarily imply that increasing latitude favours nectar secretion, as higher surplus yields may be due entirely to the longer hours of daylight during which the bees are able to gather nectar and pollen. It is, however, possible that high latitudes do favour nectar secretion, as the longer hours of sunshine lead to increase photosynthesis in plants; and the more marked differences between night and day temperatures increase the nectar yield. We do not know whether any attempt has been made to apply the work of Garner and Allard on 'long and short day plants' to the influence of the length of day on nectar secretion, but the subject is of particular interest as it may confirm the general belief that the marked superiority of the clover honey-crops in the north is partly due to increase in nectar secretion.

We have given a résumé of most of our knowledge of the influence of various factors upon nectar secretion. Although important advances have already been made we are still ignorant of the exact relationships between the flow of nectar and any one of these factors. We are left with the impression that our ideas are still at the qualitative stage, and that a great deal of work is necessary before we can express in quantitative form the true relationships of soil conditions, weather, altitude and latitude to nectar secretion. It is possible that we shall never succeed in correlating all these factors with nectar secretion, but as soil conditions are the only factors subject to human control in a given locality it is important that a serious attempt be made to study the influence of soil upon the yield of nectar. The literature devoted to bee-keeping abounds in random observations on the influence of soil conditions on nectar secretions and the yield of honey, and as these emanate from bee-keepers of long experience they deserve some attention, although they should be critically considered in the light of chemical and physiological facts. It is therefore desirable that competent bio-chemists and plant physiologists should examine the traditional beliefs of bee-keepers and conduct experiments to test their validity. On the other hand, it may be better to start from the fundamental principles of chemistry, physics and plant physiology, and thus remain free from the burden of tradition, as no doubt a great deal in bee-keeping does not rest on a true foundation.

The rôle of pollen in the life of the bee.

Nectar is the principal source of carbohydrate in the food of the honey-bee. Nectar, when converted into honey, forms laevulose and glucose which are a concentrated and readily digestible form of energy necessary for the flight and other activities of the bee.

Pollen is the source of all other foods required by the bee and it provides the material for royal jelly, for the formation of muscles and all other organs, and it is also the basis for the repair of worn-out tissues. It is evident, therefore, that pollen is essential for growth and reproduction within the hive and that it must be supplied in abundance at the time of brood-rearing. Pollen contains carbohydrates and fats, but its most important constituent is protein. It also contains the elements calcium, magnesium, iron, sodium, potassium, aluminium and manganese, as well as phosphorus and sulphur. In addition, it contains vitamins, enzymes and colour pigments.

Some idea of the amount of pollen necessary to rear brood in a year may be gleaned from the following facts. Haydack found that 3·2 milligrammes of nitrogen, derived from protein, are necessary to rear one bee. As the average nitrogen content of pollen is 3·1 per cent it follows that 100 milligrammes are required to rear one bee ; or one pound of pollen will rear 4,540 bees. Nolan has shown that a strong colony rears about 200,000 bees per annum, so that about 44 pounds of pollen are used by each colony. In the experiments of Todd and Bishop, who used pollen traps to collect the pollen loads of bees, they obtained 77 pounds of pollen from one hive. (They state that 80,000 tons of pollen could be collected in America alone in one year and used for various

purposes.) It has been estimated that 10 loads of pollen are required for one bee, so that it would take 2,000,000 loads to rear the brood in one colony each year. Todd and Bishop actually found experimentally that one colony had collected nearly one and three quarter million loads in one year.

The chemical analysis of pollen shows that its composition varies within wide limits amongst different species of plants; the protein ranges from 7·9 to 40·0 per cent; the fat from 1·5 to 23·6 per cent; the ash from 2·8 to 10·6 per cent; and the sugars from 0·8 to 11·1 per cent. The following are some analyses carried out by Todd and Bretherick:—

Plant source.	Protein.	Fat.	Sugars.	Water.	Ash.	Undetermined.
	%	%	%	%	%	%
Dandelion	11·1	14·44	34·93	10·96	0·9	27·6
Clover	20·68	3·22	30·20	13·44	5·4	26·9
Star Thistle	21·19	6·56	24·88	16·23	1·8	29·3
Charlock	22·41	13·13	28·92	9·75	2·6	23·2
Birch-brush	26·08	0·94	24·34	10·07	3·1	35·5
Blue Gum	26·2	1·38	29·96	9·09	2·7	30·6
Bermuda grass	20·44	2·37	29·33	13·34	3·1	31·5
Lodge-pole Pine	7·0	2·04	48·35	7·00	1·3	34·3

(In the above, 'Fat' should be more correctly described as ether extract, and 'Sugars' includes sugars, starch, gums and celluloses.)

It is hardly necessary to indicate the wide variations in these analyses; for example high fat content of the dandelion and the charlock and the exceptionally low fat content of birch-brush (*Ceanothus integerrimus*) and the very low protein content of lodge-pole pine (*Pinus contorta*). As we shall see later, these differences are very significant in the economy of the hive.

We have already shown that bees select the flowers which are secreting the nectar of highest sugar content within their range, and in a similar way they select the most attractive pollens—although we do not know the determining factors which lead to this selection. Pollens are known to contain traces of vitamins, for example carotin, and it is possible that if the hive is short of these essential food accessories the bees concentrate on the plants which yield pollen containing the highest vitamin content. Vansell records that cotton pollen was abundant and easily accessible in the San Joaquin Valley in September 1938, but the bees devoted their attention almost entirely to the limited supply of green pollen of the blue curls (*Trichostema lanceolatum*) found in the same neighbourhood. Similarly, the pollen on sunflower blossoms was neglected in favour of that found on spikeweed (*Centromadia pungens*). As the amounts of fats, protein, ash, etc., varies so markedly in the pollen of different plants it is possible that bees find it necessary to blend their pollen loads in order to obtain a balanced diet.

Feeding experiments, recently carried out by the Bureau of Entomology, U.S.A., with pollen added to sugar syrup indicates that there

are two phases of pollen nutrition. Egg-laying was stimulated by the liquid food supplied by the worker bees to the queen, but brood rearing is dependent on pollen reserve in the form of bee-bread. Egg-laying seems to be determined by the pollen eaten by the workers and not by the queen, as she consumes very little, if any, pollen. The queen's supply of nitrogen food appears to be supplied by the worker as a secretion, but its source is unknown. The peaks in the egg-laying periods by the queen are reached when the bees are working on pollen plants yielding pollen rich in fat, such as charlock and dandelion.

It is well known that occasionally in the midst of abundant supplies of pollen there is not sufficient food to rear bees, and this can only be assumed to be due to the absence, or deficiency, of essential foodstuffs in the pollen.

The supplies of pollen reaching the hive are determined not only by seasonal variations in the flowering of plants but also on the species of plant in bloom, as well as on numerous weather factors which vary from day to day. Certain excellent nectar plants, such as orange and fireweed, are of little value as sources of pollen; but, on the other hand, some nectar plants such as sweet clover and the sages are excellent pollen plants as well. Wide variations in the daily yields of pollen are also observed owing to the effect of weather conditions on the dehiscence of anthers. In addition, variations in temperature, cloudiness, rainfall and wind affect the activities of bees as in the case of nectar foraging, so that these effects are also reflected in the daily harvest of pollen.

It has already been mentioned that pollen grains contain various colouring materials and these fall into two classes –water soluble and oil or fat soluble. The former group colour the honey and the latter colour the wax. Thus the pollens of red maids (*Calandrinia caulescens*) and dandelion impart a yellow colour to white beeswax whereas the bright red pollen of filaree (*Erodium* spp.) has no effect on wax. It appears that the oil-soluble colouring materials liberated by wax-staining pollens are carotinoid pigments and it has been shown that the orange-coloured pigment of the pollen from mullein (*Verbascum thapsiforme*) is composed entirely of carotin.

Poisonous nectars have already been mentioned and poisonous pollens also occur. The well-known 'Bettlach May-Sickness', which is a type of bee paralysis prevalent around Bettlach in Switzerland, has recently been shown by Morgenthaler and Maurizio to be due to the pollen of *Ranunculus puberulus*, the Wood Buttercup. It is significant that bees do not usually work this plant but prefer the dandelion and cherry flower, which bloom at the same time; but if a cold spring delays these plants the bees seek pollen from the hardier buttercup. Frl. Maurizio found the poisonous principle anemonal in many species of the genus *Ranunculus*. The pollens from rhododendrons, scabious and fox-glove are also stated to be poisonous to bees. It was recently found that bees in Brewster County in Texas were poisoned by the pollen of loco-weed (*Astragalus* sp.), but it is interesting to note that bees are normally not attracted by this plant; but during the last season the pea-vine (*Vicia* sp.) was late in blooming and the bees in the absence of other pollen collected pollen from loco-weed.

Much work remains to be done on the chemical composition of pollens and its correlation with the characteristics of the species of plant from which it is derived.

Identification of pollen grains.

There are at least three important applications of the identification of pollen grains: in archaeology and studies of post-glacial history of vegetation, in the study of the cause and origins of hay-fever and in the study of honey. We do not propose to discuss here the methods of mounting and staining pollen grains; the systems of classification or their various characteristics as a wealth of information is given in the standard books written by Armbruster, Wodehouse, Zander and Yate Allen, as well as in the numerous articles by Miss Betts.

We shall confine our remarks to a discussion of pollen grains as a means of identifying the sources of nectar in a sample of honey. It will be realized that 'pollen analysis' of honey involves wide experience in the observation and measurement of pollen grains under the microscope and familiarity with the grains from the principal honey plants of the world. Such knowledge and experience can be gained only after many years systematic work on pollen grains actually collected from the flowers themselves, along with observations on these grains in honey as, under these two conditions, the apperance of the grains is not the same. In spite of the many excellent photographs and drawings of pollen grains which have been published these are not a satisfactory approach to the subject; they are, however, of much assistance and a source of encouragement when they confirm the presence of characteristic features which the beginner has seen for himself. Some pollen grains, however, are so unique in appearance under the microscope that they can be readily identified from a photograph.

Opinion is strongly divided as to the validity of the inferences which can be drawn from the presence of various pollen grains in a sample of honey. Some go so far as to maintain that the method is of little value in deducing the origin of the parent nectars, whereas others believe that the proportion of pollen grains in honey gives a reasonable indication of the proportion of the parent nectars. We cannot agree with the former attitude, as it is hardly reasonable to believe that a sample of honey in which the predominant pollen grains were those of orange, sage and manzanita had been gathered from English flowering plants. On the other hand, we are of opinion that a 'pollen analysis' of a sample of honey gives only the proportion of pollen grains present in the sample —it does not give the correct proportion of the parent nectars. It is reasonable to assume that if a sample contains appreciable numbers of pollen grains of 'manuka' (*Leptospermum scoparium*) it does contain a proportion of manuka honey, and that it has originated from New Zealand. If a sample, however, contains equal proportions of heather, fireweed and clover grains, we cannot infer that the honey has been derived from equal amounts of nectar from these three plants. In estimating the value of 'pollen analysis' as a means of determining the source of honey it is well to consider the following observations.

All nectars are not equally rich in pollen; thus Californian orange honey is singularly low in pollen content. Lime and *Fuchsia* honeys

contain few pollen grains, as the pollen from their pendant flowers falls into the air, whereas the grains in upright blossoms fall into the nectar secreted inside the corolla. Supers are not always supplied with fresh combs, thus when bees are taken to the moors for the heather flow they are often supplied with combs that had previously been full of clover honey before extraction. When the heather honey is recovered by means of a press the combs are crushed and the clover grains which had adhered to the cell walls pass into the honey. In addition, fireweed frequently grows near, or on, heather moors, and as fireweed nectar is not as rich as heather nectar in pollen grains the ratio of grains in the honey is not a true indication of the ratio of the parent nectars. Hence a sample of heather honey which, from pollen counts, appears to consist of equal parts of heather, fireweed and clover honey may be derived to a great extent from heather nectar. It frequently happens that bees store pollen in a few cells in the upper combs and if these are not removed before the extraction of the honey it is evident that pollen counts will not be reliable. Lastly, pollen grains from anemophilous plants, which yield no nectar, are found in honey samples, and these must be disregarded in tracing the origin of the nectars.

Although we have stressed the limitations of pollen analysis in its quantitative aspect, we still believe that it has considerable importance, especially in detecting the geographical origin of the honey. Recently we examined a sample of imported honey stated to be of South African origin, but it contained so many pollen grains characteristic of West African flora that we had no hesitation in stating its origin, and thus placing the honey in a lower grade than its commercial description. As another example of the application of the identification of pollen grains we quote an instance where a quantity of honey was offered for sale and the sample was examined for pollen grains by Mr. Yate Allen. He later examined a sample from the actual delivery of the honey and his observations are recorded in the following tables :—

An 'English' honey offer.

Sample offered.	% grains.	Honey delivery.	% grains.
Sainfoin	45	*Robinia Pseud-acacia*	44
White Clover	35	*Brassica* sp.	24
Lucerne.....	16	*Rhamnus Purshiana*	19
Dandelion	3	*Eucalyptus* sp.	5
Plantain (Plantago)	1	*Citrus Aurantium*	3
		Trifolium hybridum	3
		Acacia (*hastulata* ?)	2

The sample of honey as offered for sale is a typical English honey, but the pollen grains in the honey as delivered are certainly not of English origin, and from a knowledge of the local flora it may safely be assumed that the honey came from California. It is not claimed, however, that the parent nectars were gathered in the ratio of the pollen grains observed in the sample. A few years ago we purchased a carton of honey described as 'Genuine Yorkshire Heather Honey', but as the predominant pollen grains were heather, clover, manuka, rata and pohutukawa (*Metrosideros tomentosa*), we inferred it was a blend of

English heather and New Zealand honeys. We need not give any further illustrations of this particular application of the use of pollen grains.

There are still a number of peculiar honeys, the origin of which cannot be traced with certainty; for example, a green honey is sometimes obtained in Illinois, and a beautiful pink honey is obtained near Stirling and in parts of Galloway. The pink honey is stated to be derived from wild geranium, but the following 'pollen analysis' by Yate Allen shows that it is entirely free of pollen grains from this plant, so that its origin is still unknown. We also include Yate Allen's observations on a sample of New Forest ling heather honey which was claimed to be of superior purity. Pollen counts would lead one to believe that a great deal of bell heather was in bloom at the same time, and a study of its thixotropic constants revealed that it was of inferior quality compared with heather honey from the moors of Durham, Yorkshire, Devonshire and some of the Scotch Highlands, and its protein content was below 1·0 per cent, hence physical and chemical tests appear to confirm the pollen counts.

Honey identification.

Pink honey from Stirling ('Wild Geranium').

	% grains.
Gentian	23
Polygonum sp.	17
Blackberry	13
Mustard	10
Scabious	10
Dog Rose	8
Willow-herb	5
Thyme	5
Thistle	5
Pennywort	2
Sainfoin	2

New Forest 'Ling' honey.

	% grains.
Bell Heather	30
Ling	25
White Clover	20
Hawkweed	13
Thistle	5
Mint	3
Sweet Chestnut	2
Blackberry	2

We have expressed our opinion of the value of pollen counts and identification of pollen grains in honey, but we realize that our opinions do not agree with those of several experts on the subject.

The number of pollen experts in this country is limited, and apart from Miss Betts and Mr. Yate Allen, I am not aware of any others who are competent to identify pollen grains in samples of honey from any part of the world. As the study of honey pollens is of such importance as well as of great interest it is to be hoped that a number of young botanists will take up the subject seriously. The study of pollen grains in relation to hay fever is of the greatest importance, and this subject is now being systematically investigated by Mr. H. A. Hyde and Dr. Williams at Cardiff, who have developed an excellent technique for the microphotography of pollens and are producing a collection of photographs of English pollens which will be of much value in pollen studies. Mr. V. H. Chambers is making a valuable collection of pollen slides, with particular reference to the bees of the genus *Andrena*. There may be others, of whom I am not aware, but it is to be hoped that the interest in pollen grains in this country will be considerably extended.

Bees in relation to orchard and farm crops.

It has already been stated that, in England and Wales, the value of bees as pollinators greatly exceeds the value of the surplus honey obtained from the hives. This is equally true of the great honey producing countries of the world; thus E. F. Phillips estimated, in 1911, that the value of the honey and wax obtained in America amounted to about £5,000,000, but the value of the pollinating services of the bees was at least five times this figure. The value of the bees in pollinating sunflower plants, buckwheat and orchard blossoms in Russia is about £40,000,000 annually. Such an eminent authority as Professor Rea, of Cornell, maintains that 'without honey bees it is doubtful whether America would have sufficient to eat', and he has offered a great deal of evidence in support of this statement.

Effective pollination is essential for successful set of seed, but it is not generally recognized how important the services of insects are in this process. The following table is based on Hutson's observations on the extent of pollination of fruit blossoms of plants enclosed in a 12-mesh wire screen cage in which was placed a hive of bees, compared with neighbouring plants, similarly screened, but not supplied with bees. The ground inside the cages was covered with cheese cloth. After the blooming period was over the blossoms which did not set fruit fell upon the cheese cloth and were counted, as were the set fruits. As cranberry blossoms persist even if not pollinated this simplified the method for these plants.

Fruit trees in screened cages.

	Total blossoms.	Fruit set.	% Fruit set.
Pears.			
Trees with bees	8751	428	4·8
Trees without bees	6479	7	0·1
Apples.			
(*a*) 'Wealthy'			
With bees	3475	591	17
Without bees	3675	148	4·02
(*b*) 'Jonathan'			
With bees	2758	238	8·4
Without bees	1985	16	0·8
Cranberries.			
With bees	2385	1335	56
Without bees	2184	185	8·4

It is not necessary to make any comments on these results, as the influence of the presence of bees in the cages is very marked in each experiment.

Dunham found that alsike and other clovers, which are practically self-sterile, enclosed in cages so as to exclude insects, produce only from one to three seeds per head, but under maximum honey bee pollination alsike enclosed in cages, along with bees, yielded from 120 to 155

seeds per head. He has also shown that, in Iowa, natural pollinating insects, such as bumble-bees, etc., are too few to ensure efficient pollination, and where honey-bees are absent the farmers cut fields of alsike clover for hay because of the poor set of seeds. If, however, fields of alsike clover are within a mile of a commercial apiary 40 to 90 seeds per head of clover are obtained; as such a field contains from 300 to 500 million florets per acre, we can appreciate the value of the activities of bees.

The experiments in screened cages, of course, are not comparable with natural conditions. In the cage the bees are forced to devote their attention to one particular type of blossom, whereas in the field they are able to select flowers according to their own choice and can roam from one species of plant to another. It is fairly well established, however, that bees display the remarkable trait of 'flower-fidelity', that is, they remain constant in their attention to one species of flower as long as these flowers continue to secrete attractive nectar, or pollen. The bee does not roam at random from an apple blossom to a pear blossom or from a sainfoin flower to a clover flower, but continues to work on the apple or the sainfoin until a more attractive source of nectar or pollen is available. (We cannot enter here into the field of 'bee-language' and the methods by which news of more attractive supplies reach the hive, but details will be found in the papers of von Frisch and Francon.) As the trait of 'flower-fidelity' is of such importance in pollination of flowers it is of interest to refer to some of the observations made by Miss Betts on the constancy of the pollen-collecting bees. We cannot do justice to the long and painstaking work here, but must refer you to the original paper. Miss Betts examined the contents of the pollen-loads of bees under the microscope and identified the source of pollen in each load; in 1910–1912 she examined 3,019 pollen loads, and of these only 195 (or 6·4 per cent.) were mixtures of two or more pollens; in 1925–1927 she continued the work, and of 916 loads examined only 25 (or 2·8 per cent.) were mixtures. It may, therefore, be reasonably assumed from these results that bees show flower fidelity to a remarkable extent.

It is not surprising, therefore, that the pollinating activities of the honey-bee have been fully recognized in America and that it has become customary for fruit growers to hire colonies of bees during the blossom period and distribute hives symmetrically about their orchards. In order to obtain the maximum set of seed they also plant 'bouquets' of suitable trees, in order to make certain of cross-pollination in varieties of fruit trees inadequately fertile to their own pollen or pollen of their own race. Thus, in New York State alone 15,000 colonies of bees are rented annually for use in orchards, in addition to the many thousands of hives kept permanently by the growers in and around the orchards. As regards fruit growers in this country, C. G. Butler makes the following very significant remark:—'The small back-yard bee-keepers scattered throughout the length and breadth of Britain play a most important part in providing the necessary pollinating insects. There is no evidence, however, of any marked concentration of bee-keeping in the predominantly fruit growing area'. One may infer from observations

made during tours throughout the country that there are not sufficient bees in England and Wales to obtain the maximum possible setting of fruit and seed.

It is of interest to refer again to the competition amongst blossoms for bee visitors and that the selection by the bee is determined by the sugar content of the nectars. In the Pacific North-West, for example, bees prefer the mustard blossoms to pear blossoms in the same neighbourhood, so that it is necessary to replace mustard by some other crop which blooms after the pear blossoms have been pollinated. Vansell quotes an interesting case where bees in a pear orchard neglected the nectar in the pear blossoms and flew to an apple orchard a mile and a quarter away in order to collect the rich nectar in 'Delicious' and 'Steel's Red Apple' blossoms in which the sugar content ranged around 50 per cent, compared with the pear blossom nectar of 3 to 20 per cent content.

Effective pollination is essential for clover seed production. At one time Central New York State had a flourishing clover seed business, but in the early 1890's the yield of seed rapidly declined and the farmers were unable to trace the cause. It was later shown that the decline coincided with an epidemic of European foul-brood disease which ruined the prosperous bee-keeping industry. At this time agriculture and bee-keeping were rapidly developing in the Middle West, where both industries still thrive to their mutual advantage.

In the pasture development programme of the State of Florida it has been found that one of the principal problems has been the failure of clovers to re-seed to a sufficient degree. The introduction of a higher bee population would undoubtedly assist in overcoming this problem.

We hear and read a great deal about the post-war development of grassland and ley farming in this country, but so far no reference seems to have been made to the need of increasing the number of colonies of bees which will be required to pollinate the enlarged acreage of clover plants and thus ensure an abundance of home-grown seeds.

Honey plants for the future.

There are many aspects of bee-keeping in which botanists could take a theoretical as well as practical interest : one of the most important aspects is the development of new honey plants as well as the introduction of honey plants from other regions which would flourish in Great Britain. In Russia, for example, extensive work has been done on the possible improvement of the honey flora and the selecting and breeding of nectar and pollen plants with increased nectar yield.

Abundance of nectar flow is probably the most important single factor in establishing a prosperous bee-keeping industry. So far we have accepted the natural nectar secreting capacities of plants and we have made no effort to improve their efficiency as a source of nectar. As long as we remain ignorant of the factors which determine nectar flow, under our own particular climatic conditions, we cannot expect to make any fundamental advances in improving bee pastures ; we can only introduce honey plants from other parts of the world ; but this problem, in itself, deserves attention. It is important, therefore, to determine

the soil factors which influence nectar secretion. It is possible, even probable, that optimum conditions during growth and for reproduction during bloom are also the optimum conditions for nectar secretion; so far this assumption has not been proved and no one has investigated the influence of trace elements on the yield of nectar. It would be of great interest if botanists and bio-chemists could co-operate and determine the value of MacLachlan's theory; the theory rests purely on correlation of weather and surplus honey obtained from the hive, but data obtained under experimentally controlled atmospheric conditions and quantitative determination of the actual flow of nectar would be much more convincing.

By artificial selection and breeding many valuable advances have been made in the economic development of plants; for example, the sugar content of the beet and sugar cane have been increased, the quality and yield of rubber latex have been improved, the flavours and beauty of fruit have been enhanced, the yield and character of oats and wheat have been modified. It is probable that equally important advances could be made in the development of nectar secreting plants. We have already referred to the differences in the sugar content of varieties of the same fruit and its relation to the degree of pollination by bees. It may be possible to take advantage of these observations to improve the quality and yield of fruit and at the same time improve the nectar yield.

In many parts of England there is a spring honey flow from trees such as cherry, apple, chestnut and hawthorn, but this is followed by a dearth of nectar extending for three or four weeks, described as 'the gap in June', until the clover blooms. This period represents an important loss to the bee-keeper: it involves not only a dearth of nectar but it reduces brood-rearing at a most important period. If a suitable plant, blooming between the hawthorn and the clover, could be found it would produce a marked increase in the surplus yield of honey. Wedmore recently drew attention to this serious gap in June and expressed the hope that public bodies would plant trees and shrubs not only for their ornamental appeal but also for their utility as a source of nectar as part of the post-war reconstruction policy. He emphasizes the difficulty of finding suitable plants but, at his request, the staff at Kew have been making observations on the activities of bees on various trees and shrubs suitable for this country, which are found in the Gardens. They have already made several suggestions, and it is to be hoped that some of these can be adopted after the war. Wedmore observed that bees were much attracted by the flowers of white bean, rosemary and Balkan sage in his garden. He adds the interesting remark that their appeal to bees varies from season to season.

Wedmore refers to white and yellow sweet clovers as honey plants, and it is of interest to recall that, at one time, in America sweet clovers were regarded as a weed and in many States laws were passed inflicting penalties for planting sweet clovers. When the yields of corn in the Red River Valley declined to the stage where rotation of crops became essential it was found that neither alsike nor red clover gave dependable crops, but sweet clover was an ideal plant for restoring the fertility of the soil. Since that time yellow sweet clover has become the supreme

honey plant of the northern regions of America. We have seen yellow sweet clover growing in abundance on waste land in the neighbourhood of oil mills in the North of England, where it has been introduced amongst imported cotton seed. We do not know whether yellow sweet clover has any possibilities as a honey plant in England.

Red clover (*Trifolium pratense*) presents a range of problems to the botanist interested in the bee-flower relationship. The value of the honey-bee as a pollinator of this self-sterile plant is not generally appreciated because a number of bee-keepers, and others, believe that because the tongue of the honey-bee is too short to reach the nectar in the long corolla tube there is no inducement to visit red clover flowers.

The recent work of Dunham, in Ohio, and of Butler, in England, shows that honey-bees are most efficient pollinators of red clover. Dunham counted the number of pollen grains contained in flowers unvisited and also in flowers pollinated by the honey-bee and found, on an average, 1,153 grains in the unpollinated and 148 grains in pollinated flowers—in other words, the honey-bee carries away about 1,000 pollen grains from each flower. The average number of grains in pollen loads collected from red clover was 347,500, so that the bee visits 347 flowers to collect one load of pollen, and it takes 28 minutes to gather this load. The corresponding figures obtained by Butler were : 284,000 grains, 284 flowers, and 20 minutes.

Butler examined the pollen loads from 100 bees under the microscope and identified each individual pollen grain, and only in seven loads were any grains other than those of red clover found. This is another confirmation of the remarkable flower-fidelity of the honey-bee.

He also found that 60 per cent of the bees were deliberately foraging for nectar and 40 per cent for pollen when working on red clover. It was also found that there was a peak in the number of bees visiting white clover for pollen between 12 noon and 3 p.m. ; for red clover there were two peaks, one between 10 a.m. and noon, and the other between 3 p.m. and 5 p.m. As these peaks are often observed in a large variety of flowers it would be of interest to determine the factors which influence the dehiscence of pollen grains at different times of the day

Dunham found that 30 species of insects were concerned in pollinating red clover, but that 82 per cent of the flowers were pollinated by honey-bees, 15 per cent by bumble bees and 3 per cent by the remaining species of insects. No comparable data were obtained by Butler, but as such large numbers of honey-bees were found on red clover fields at certain times it appears probable that they are responsible for the pollination of a large proportion of the crop.

Stapledon maintains that ' there is little doubt that for use in Britain, red clover seed harvested in Britain gives plants of more prolonged duration than seed from oversea sources '. It is, therefore, of great importance that in the post-war period sufficient bees will be available in this country to ensure abundant sets of red clover seed.

The seeding capacity of an acre of red clover is about 12 bushels, and as there are 16,000,000 seeds in a bushel one obtains some idea of the number of visits that must be made by honey-bees in the cross-pollination of an acre of red clover. Nevertheless, if no other nectar or pollen sources are available, a colony with a strength of 10,000 foraging

bees could ensure 2½ bushels of seeds per day. In spite of the prosperous bee-keeping industry in the U.S.A. the yield of red clover seed per acre is only a little more than one bushel, hence the present high price of this seed.

Stapledon's remark on the relative merits of red clover seeds of different origins is of interest because it may have some application in the development of forage plants of better service to bee-keeping. Paddock in Iowa has found differences in sweet clover grown from Iowa seed and from Minnesota seed; plants grown from the latter bloomed earlier than plants from local seed and therefore influenced the yield of honey—the value of a nectar plant to bee-keeping is not determined completely by its nectar yield and sugar content, but also by the flowering time of other nectar plants, so that if a plant can be adapted to bloom during a break in the local flora its value is greatly enhanced.

The mean length of red clover corolla tubes according to Dunham is, in Ohio, 9·5 mm.; Butler found a value of 9·6 mm. at Rothamsted, and we found the same value in Yorkshire. The average length of the tongue of the honey-bee is 6·3 mm. (that is, one quarter of an inch); but as it can thrust its head a distance of 1·1 mm. into the opening of the corolla and 'stretch' its tongue 0·5 mm., its effective reach in a red clover corolla is 7·9 mm., or 1·7 mm. shorter than the corolla tube. Before the honey-bee can collect any nectar it is, therefore, necessary for it to accumulate to a depth of 1·7 mm. Butler found that honey-bees collected nectar in red clover about once in four or five days, and these occasions followed nights of heavy dew. As the bees limit their attention to nectars containing at least 17 per cent of sugar, it is evident that absorption of dew must not be excessive. It is generally believed in America that better set of seed is obtained in red clover during a season of dry summer, as this condition leads to corolla tubes of shorter length, so that the honey-bees are able to gather nectar from a higher proportion of flowers.

As red clover is such an important forage crop many attempts have been made to overcome the problem of the excessive length of the corolla tubes. In Russia many experiments have been made to breed bees of longer tongue length, and, to some extent, the work has been successful. On the other hand, the most promising results have been obtained by breeding a variety of red clover with shorter corolla tubes. Zofka, a Bohemian plant breeder, has succeeded in breeding a new variety in which the length of the corolla tube varies from 5 mm. to 8·5 mm. in different heads with an average of 6 mm. The nectar is, therefore, within easy reach of the bee. Sufficient seeds were obtained to plant a tenth of an acre of Zofka clover in the Iowa Agricultural Experimental Station and the plants were found, by Paddock, Pellet and Martin, to withstand heat, drought and the attack of leaf hoppers as well as most red clovers, and the nectar reached a depth of 2 mm. in the corolla tubes. Long observations on the behaviour of bees showed that they could easily reach the nectar. The bees also gathered pollen from the plants and the set of seed was superior to that from the usual red clovers; it averaged from 50 to 60 seeds per head and the record was 132 seeds.

It is not claimed that Zofka clover has completely overcome the red clover problem, but the preliminary observations show that it has

considerable prospects of success. The new plant is also an excellent illustration of the mutual advantages which agriculture and bee-keeping obtain from the co-operation of the botanist and the bee-keeper.

Conclusion.

We have presented a number of facts which are involved in the study of the bee flower relationship, and many of these still await a satisfactory explanation. It is probable that a botanist or a bio-chemist would have treated the subject in a very different way, but it should be recalled that our interest was first aroused by the peculiar physical properties of heather honey. As soon as it was proved that these conditions arise from the presence of an abnormal amount of protein we were faced with the more serious problem of explaining the origin of protein in heather nectar, and were thus involved in the study of nectar secretion in plants in general. This new problem still awaits solution, and until we have discovered the fundamental principles of nectar secretion and the factors which determine the composition of nectar we cannot hope to explain the presence of protein in heather honey. There are many other problems associated with nectar, pollen and honey, and it is very desirable that a number of biologists should take an interest in them.

I should like to express my gratitude for their valuable assistance to Miss A. D. Betts, Professor K. W. Braid, Mr. E. G. Burtt, Dr. C. G. Butler, Professor A. C. Chibnall, Mr. J. Cunningham, Dr. E. M. Delf, Professor E. F. Phillips, Messrs. R. Frow, J. Sydney Giles, C. B. Gooderham, L. Harker, J. I. Hambleton, L. Illingworth, D. Morland, Dr. O. W. Park, Professor F. B. Paddock, Dr. M. V. Rayner, Mr. E. R. Root, Dr. G. W. Scott Blair, Mr. Tickner Edwardes, Mr. Vansell and Mr. Yate Allen. In particular I should like to thank Dr. H. S. Paine, Chief, Agricultural Chemical Research Division, and his associates at Washington for their generous gifts of honey samples and of the literature published by their department during the last ten years.

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Discussion.—

Mr. H. A. Hyde. I was much interested in Mr. Pryce-Jones's paper and hope that it will stimulate further research into the problems he raised. In particular there is room for work on the identification of pollens. I have been interested in the pollen analysis of peats ; Dr. D. A. Williams and I have worked together on atmospheric pollen ; and we have both examined honey for pollen. The pollen analysis of peats, as at present practised, necessitates the use of drastic techniques in order to isolate the pollen ; that of honey and of pollen deposited from the atmosphere does not. We have compared the results of preparing standard pollen slides with and without the use of acetic anhydride and/or caustic alkali, and have found that these reagents caused varying degrees of swelling and distortion of the exine in addition to partial or (after acetolysis) complete destruction of the intine and contents. Standard slides made by such methods are likely to be misleading when used to identify pollens centrifuged from honey or deposited from the atmosphere. We think, therefore, that the type of preparation to be used as an aid to identification should vary according to the object for which it is made ; pollen analysts of peat will prefer standard slides made by acetolysis ; workers on pollens derived from honey or from the atmosphere will find it an advantage to use standard slides made by the simple process of staining and mounting in glycerine jelly. Museum collections should contain slides of each species, made by both methods ; or if by one only, then the latter method is preferable as being easier and of wider utility.

Dr. R. Melville said that Mr. Pryce-Jones had raised a great many interesting points that might be discussed. He had found that pollen grains could be separated readily from diluted honey either by sedimentation or centrifuging. The separated grains could be mounted in the usual way in glycerine jelly.

A reference collection of pollen slides was now being made at Kew which should be valuable for identifying pollens concerned in hay-fever, and pollen analysis, as well as honey pollens. It would also have considerable taxonomic value.

Mr. Cartwright Farmiloe suggested that it would be useful to apply some of the chemistry of aromatic bodies to various problems of honey and particularly to those of propolis. Bees seeking propolis will at times alight on freshly applied varnish or try to remove fresh paint. When sections of honey become what is usually termed ' travel-stained ', through being left on the hive too long after the harvest, there is a definite attempt by the bees to give a very thin coating of propolis (or varnish, as it were) to the cappings of the comb in order to protect still further the stored honey from the atmospheric changes of winter.

PROCEEDINGS OF THE ANNIVERSARY MEETING
24 May 1943

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 13 May 1943, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Professor Y. Bhâradwâja, Dr. N. Polunin, Dr. Annie Porter and The British Council.

On behalf of Mr. H. J. Howard, F.L.S., the Botanical Secretary exhibited a living specimen of *Senecio squalidus* from Norwich, where it is now extremely abundant, and two plants of *S. vulgaris* with intermediate characters, which grew in association on the Castle Mound.

The following Fellows signed the Obligation in the Book of the Charter and Bye-Laws and were admitted :—Dr. Raphael Ernest Grail Armittoe and Dr. James Desmond Smyth.

Read for the second time certificates of recommendation of the following candidates for Fellowship :—in favour of Alec Lindsay Poole, Leon Raymond Hayward and William Homan Thorpe.

Candidates for membership were balloted for and elected :—

As Fellows :—Benjamin Thornton Cromwell, B.Sc., Ph.D., Julia Hannah Pheasant, B.Sc., and William Percy Jones.

As Foreign Members :—Prof. Carl Johan Fredrik Skottsberg and Dr. Alfredo Ramalho.

As Associates *honoris causa* :—Thomas William Burton and Charles Biddolph.

As an Associate :—Richard John Harrison, B.A.

The Bye-Laws regulating the Election of Council and Officers having been read by the Assistant Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Dr. J. Hutchinson, Mrs. J. R. Sealy and Mr. G. W. Harris as Scrutineers of the Ballots.

The following Financial Report was given by the Deputy Treasurer, and the Accounts of the Society (as printed on pp. 176–179), duly audited, for the year 1942–43 were laid before the meeting.

The Treasurer's Report.—Copies of the printed reports for the financial year which ended on 30 April last are before you. They were prepared by the Professional Auditors, who certify as to detail, and they have been passed by the Audit Committee and accepted by Council.

You may wish me to comment briefly on a few matters.

Treasurer's Accounts for the

(Presented at the Anniversary

Receipts and Payments of the Linnean Society

General

Receipts	£	s.	d.	£	s.	d.
To Balance at 1 May 1942 :—						
Current Account at Bank	155	5	5			
Deposit Account Post Office Savings Bank	1330	0	0			
Cash in hand	4	17	9			
				1490	3	2
,, Admission Fees				24	0	0
,, Arrears of Annual Contributions	97	3	7			
,, Annual Contributions for year	1925	4	0			
Do. in advance	50	8	0			
				2072	15	7
,, Composition Fees				68	3	11
,, Interest on Investments (including Income Tax recovered)				279	2	5
Do. Deposit					8	8
Do. Post Office Savings Bank Account				77	7	3
,, Sales of Publications :—						
Transactions	1	10	0			
Journals	33	19	6			
Proceedings	15	5	1			
				50	14	7
,, Donations in aid of Publications				300	0	0
,, Donations for General Purposes				7	1	0
,, Miscellaneous Receipts				27	11	2
,, £1000 Eastern Bengal Railway 4 per cent. Irredeemable Debenture Stock, acquired by H.M. Treasury				1044	0	0
				£5441	7	9

Library

Receipts	£	s.	d.
To Balance 1 May 1942	239	2	11
,, Interest on Investments (including Income Tax recovered)	47	6	5
,, Donation		4	9
,, Deposit Account Interest		14	10
	£287	8	11

Fellows Postal

Receipts	£	s.	d.
To Balance at 1 May 1942	51	4	1
,, Deposits during year	1	4	0
	£52	8	1

YEAR ENDED 30 APRIL 1943

Meeting, 24 May 1943)

from 1 *May* 1942 *to* 30 *April* 1943

Account

PAYMENTS	£	s.	d.	£	s.	d.
By Coal, Electric Current, and Gas				70	19	11
,, Repairs: Sundry				6	0	6
,, Taxes and Insurance				54	16	8
,, Miscellaneous Printing and Stationery				117	11	10
,, Petty Expenses and Postages				110	6	10
,, Fire Watching Expenses				64	11	11
,, Publications :—						
Printing	364	5	10			
Illustrations	13	12	0			
Distribution	40	15	9			
				418	13	7
,, Salaries, Wages, etc. (including £26 4*s.* 11*d.* Travelling Allowances)				1026	4	7
,, 'Zoological Record' Donation				15	0	0
,, War Damage Insurance (Library, Furniture and Fittings)				198	15	0
,, Staff Annuities (Annual Premiums)				100	0	0
,, Purchase of £1269 2*s.* 4*d.* 2½ per cent. Consolidated Stock				1044	0	0
,, Transfer to Reserve Fund for Library and Renewals				850	0	0
,, Balance at 30 April 1943 :—						
Current Account at Bank	*202	0	11			
Deposit Account Post Office Savings Bank	1157	7	3			
Cash in hand	4	18	9			
				1364	6	11
				£5441	7	9

* Includes £68 3*s.* 11*d.* Composition Fees awaiting investment.

Account

PAYMENTS	£	s.	d.	£	s.	d.
By Periodicals				49	1	11
,, Binding				57	0	0
,, Books				20	8	0
,, Purchase of £107 2*s.* 1*d.* 2½ per cent. Consolidated Stock (Stebbing Bequest)				88	9	8
,, Balance at 30 April 1943 : Current Account	2	9	4			
Deposit Account	70	0	0			
				72	9	4
				£287	8	11

Account

PAYMENTS	£	s.	d.
By Balance at 30 April 1943	52	8	1
	£52	8	1

Separate Account

Receipts

	£	s.	d.	£	s.	d.
To Balance at 1 May 1942 :—						
Westwood Fund	39	13	3			
Trail Award Fund	25	19	2			
Crisp Award Fund	21	16	8			
Hooker Lecture Fund	121	2	2			
Goodenough Fund	14	10	7			
Minchin Fellowship Fund	116	5	0			
Carnegie Corporation Grant	1516	17	7			
				1856	4	5
,, Interest on Investments (including Income Tax recovered) :—	£	s.	d.			
Westwood Fund	10	17	1			
Trail Award Fund	3	10	0			
Crisp Award Fund	10	4	8			
Hooker Lecture Fund	21	17	10			
Goodenough Fund	8	12	1			
Minchin Fellowship Fund	2	5	5			
Staff Pension Fund	32	5	3			
				89	12	4
,, Transfer from General Account to Reserve Fund (Library and Renewals)				850	0	0
,, £315 4*s.* 5*d.* India 3½ per cent. Stock acquired by H.M. Treasury				315	4	5
				£3111	1	2

Payments

	£	s.	d.	£	s.	d.
By Westwood Fund :—						
Cost of Illustrations				6	2	6
,, Goodenough Fund :—						
Transferred to Annual Contributions				16	10	0
,, Minchin Fund :—						
Transferred to Annual Contributions				8	0	0
,, Carnegie Corporation Grant (Photography, etc.)				764	0	6
,, Staff Pension Fund :—						
Purchase of £31 10*s.* 5*d.* 3 per cent. Savings Bonds 1955/65				32	5	3
,, Minchin Fund :—						
Purchase of £100 3 per cent. Savings Bonds 1960/70				100	0	0
,, Purchase of £380 10*s.* 6*d.* 2½ per cent. Consolidated Stock				315	4	5
,, Balance at 30 April 1943 :—						
Westwood Fund	44	7	10			
Trail Award Fund	29	9	2			
Crisp Award Fund	32	1	4			
Hooker Lecture Fund	143	0	0			
Goodenough Fund	6	12	8			
Minchin Fellowship Fund	10	10	5			
Carnegie Corporation Grant	752	17	1			
Reserve Fund	850	0	0			
				1868	18	6
				£3111	1	2

Investments on 30 April 1943

General Account

£	s.	d.			Market Value 30 April 1943 £	s.	d.
1000	0	0	3½ per cent. London County Consolidated Stock 1958–68	@106	1060	0	0
1000	0	0	Great Western Railway 4 per cent. Debenture Stock	@114	1140	0	0
312	0	0	London Midland & Scottish Railway 4 per cent. Preference Stock	@ 79½	248	0	10
338	6	8	3½ per cent. War Stock	@103⅜	350	11	11
1000	0	0	3 per cent. Defence Bonds	@100	1000	0	0
2199	18	6	4 per cent. Australian Stock 1961–64	@107½	2364	18	5
200	0	0	3 per cent. War Stock 1955–59	@101	202	0	0
1139	13	0	3 per cent. Savings Bonds 1955–65	@100½	1145	7	0
1269	2	4	2½ per cent. Consolidated Stock	@ 81½	1034	6	8
					£8545	4	10

Library Account

£	s.	d.			£	s.	d.
450	0	0	Forth Bridge Railway 4 per cent. Stock (Bentham Bequest)	@108	486	0	0
530	0	0	East Indian Railway 3½ per cent. Debenture Stock (Tagart Bequest)	@101½	537	19	0
103	12	5	Surrey County 3 per cent. Stock 1961–66 (Wakehurst Bequest)	@ 99⅔	103	2	1
191	12	7	4 per cent. Australian Stock 1961–64 (Walker & Morey Bequests)	@107½	206	0	1
107	2	1	2½ per cent. Consolidated Stock (Stebbing Bequest)	@ 81½	87	5	10
					£1420	7	0

Separate Account

£	s.	d.				£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent. " B " Stock (Westwood Bequest)	@ 98	227	12	1
	667	14	2	Ditto ditto (Hooker Lecture Fund)	@ 98	654	7	1
	163	11	5	Ditto ditto (Goodenough Fund)	@ 98	160	6	0
	100	0	0	New South Wales 3½ per cent. Stock, 1930–50 (Trail Award Fund)	@ 99	99	0	0
	409	11	1	2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 81½	333	15	9
£380 10 6	156	7	2	,, ,, ,, (Westwood Fund)	@ 81½	127	8	8
	74	14	6	,, ,, ,, (Hooker Lecture Fund)	@ 81½	60	18	0
	149	8	10	,, ,, ,, (Goodenough Fund)	@ 81½	121	15	10
	231	10	5	3 per cent. Savings Bonds 1955–65 (Staff Pension Fund)	@100½	232	13	7
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@100¼	100	5	0
						£2118	2	0

B. BARNES, *Deputy Treasurer*.

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1943, and found them correct. We have verified the Investments and Bank Balances.

Dated this 17 May 1943.
W. B. KEEN & Co., *Chartered Accountants*,
224 Regent Street, London, W.1.

E. S. RUSSELL,
E. M. WAKEFIELD,
D. J. SCOURFIELD,
R. H. BURNE,
I. HENRY BURKILL. } *Audit Committee.*

The War Damage Contribution, while still a heavy charge on the Society, has cost rather less than was expected, and there is reason to hope that it will not, at any rate, cost more in the current year. The other expenses arising directly from the War (payments to Fire Guards and the like) remain as an unavoidable and unproductive charge on our funds, and so must be borne.

The difficulty of collecting the Annual Contributions from Fellows overseas remains with us, and there is some £530 owing to the Society. During the financial year, £97 of arrears came in, and, we hope, as time goes on, and especially when conditions in Asia improve, a substantial portion of the arrears may come in. Anything that can be done to collect the money is being done.

During the year, the Society has adopted certain changes in the Bye-Laws which will make it easier for Fellows of the age of 65 and over to compound their subscriptions and retain their Fellowship. A Treasurer is bound to look suspiciously at any scheme which diminishes the annual income of the Society, even when there is a prospect of long-range benefit. The new scheme has not been in operation long enough to make it possible to estimate how much it will affect our annual income, but it is bound to cause some diminution. May I perhaps be allowed to say that I hope that any Fellow who is thinking about compounding, will think well before doing so. The whole matter is one of balance between present needs and the benefit the Society will get in the future by an increase in its investments, for all money received in composition fees will be permanently invested.

Your Council has agreed to the setting aside of £850 as the beginning of a reserve fund to meet post-war expenditure, and if the finances of the Society allow, the reserve will be augmented during the present year.

Shortage of paper has limited the volume of our publications during the year under review, and expenditure on the head has been very low. There is a good deal of material in hand, much of it already with the printers, and the probability is that we shall spend more this year.

It is a pleasure to acknowledge some generous donations from the Royal Society : we have had £300 from funds they administered, namely, £200 from the Rockefeller Grant, and £100 from the Parliamentary Grant. One of our oldest lady Fellows, Dr. Catherine Raisin, very generously sent £6 for the use of the Society.

The compulsory purchase by the Government of some of our Indian investments is duly recorded in the accounts. The money has been invested in 2½ per cent. Consols, but, though we got those on favourable terms, the new investments will not bring in as much as did the old. The loss of income is another consequence of the War.

Our Assistant Secretary has kept a careful eye on general expenditure, and nothing has been spent except on what is essential to the carrying on of the affairs of the Society. The economies made are not large, but, in these days of falling income and rising prices, they are very welcome.

We have a comfortable balance in hand, which, with the income to be expected during the current year, should see us safely through to this time next year, when, perhaps, the Treasurer may be able to present a cheerful prospect of renewed activity and growth.

On a motion by Lt.-Col. W. P. C. Tenison, D.S.O., seconded by Mr. G. W. Harris, the Report and Statement of Accounts were adopted.

The Librarian and Assistant Secretary presented his Report, as follows :—

THE LIBRARIAN & ASSISTANT SECRETARY'S REPORT.

List of the Society.—Since the last Anniversary Meeting the Society has lost 21 members. The detailed statement is as follows :—

13 Fellows by death.—Dr. E. J. Allen, C.B.E., F.R.S., Surgeon Rear-Admiral W. G. Axford, C.B., A. W. Bartlett, M.A., Sir Edwin J. Butler, C.M.G., C.I.E., F.R.S., H. E. Forrest, Dr. E. E. Galpin, Miss A. M Geldart, The Most Hon. The Marquess of Headfort, C. C. A. Monro, M.A., J. Graham Murray, Dr. R. S. Rogers, T. H. Wardleworth, E. J. Wortley, C.M.G., O.B.E.

1 Associate by death.—Dr. C. Davies Sherborn.

7 Fellows by withdrawal.—Miss Doris Richardson, Miss Rachel Harries, M.Sc., Dr. W. R. B. Oliver, Miss Eileen Sutton, T. E. Hughes, R. I. Pocock, F.R.S., Miss C. Vivian.

During the Session 17 Fellows, 2 Foreign Members, 2 Associates *honoris causa* and 1 ordinary Associate have been elected. Of the 17 Fellows elected, 13 have qualified. The present number on the List of Fellows is 628, with 4 Fellows elected but not yet qualified.

Library.—Between 1 May 1942 and 30 April 1943, 36 books, 232 parts of periodical publications, and 63 reprints have been presented. During the same period the number of volumes bound was 154.

The number of volumes borrowed by Fellows and Associates was 536 and by the National Central Library 273. 388 signatures were recorded in the Library Visitors' book.

A complete set of the Linnean Society's serial publications has been received as a donation from the India Office, and has been transferred to a safe place of storage as a reserve set for the Society's Library.

Linnaean Collections.—During the early part of the Session the microfilm photographic record of the Collections was continued and completed. The more important inscriptions on the versos of the sheets in the Herbarium have now been included.

One set of the positive films has reached the Royal University, Uppsala, and two sets sent to Harvard University have been safely received.

My compilation of the Catalogue of the Linnaean Herbarium has been continued, as in last Session, out of official hours ; and considerable progress has been made. The printing of the Catalogue, when ready, has been sanctioned by the Council ; and part of the balance of the Carnegie Corporation's grant has been ear-marked for that purpose. The lists of specimens sent to Linnaeus, which had been selected specially for the photographic record, have proved a source of valuable data additional to the information written on many of the sheets of the Herbarium. In many hundreds of instances it is now possible to give

not only the provenance of specimens but to add the dates when Linnaeus received them. Some valuable lists have also been found in printed works, as for instance, in the Linnaean thesis, 'Plantæ Surinamenses', where I discovered that the numbers printed against the plant-names were the collector's numbers and collated in most instances with numbers written by Linnaeus on sheets of the Herbarium.

In order to carry out correct attributions of the handwritings on the labels and of other inscriptions, an intensive study of numerous handwritings of the Linnaean period has been necessary. One of the subsidiary results of this study has been that I am now able to attribute to Pehr Osbeck a MS., 'Defecta Herbarii', the writer of which hitherto had been unidentified and the MS. in no way connected with the Linnaean Herbarium. This MS., which Osbeck, after his return from China, must have prepared at Linnaeus's request, is a survey of Linnaeus's Herbarium. Its purpose appears to have been to enable some of Linnaeus's other students, for instance Solander, to collect specimens of plants still lacking in the Herbarium. Its date can be stated to be approximately 1755, but this may have to be modified when the MS. has been studied in greater detail.

The President addressed the Meeting on the welfare of the Society as follows:—

The President's Review.—In this, the fourth year of the War, the activities of our Society have gone on quite normally: the usual number of meetings have been held and attendances have been good. There is little change in our membership; we have lost 25 Members by death or withdrawal and welcomed 22 newcomers to our ranks; the total number of Fellows now stands at 629, compared with 632 at the end of the last Session. Among distinguished Fellows removed from our midst by death we especially mourn Dr. E. J. Allen, for so many years the Director of the Plymouth Laboratory, and Sir Edwin Butler, the founder and first Director of the Imperial Mycological Institute.

During the year the Council has undertaken a complete revision of the Bye-Laws, and the result of their labours, as confirmed at the General Meeting held on 25 March 1943, is embodied in the new edition published last month, copies of which are available to any member on application. Apart from a number of minor alterations and improvements, mainly verbal or consequential upon major alterations, the important changes relate to Chapter 5, dealing with the Associates, and Chapter 8, which deals with the manner of election of Council and Officers. We have now two classes of Associates: one limited to 25 in number and corresponding exactly to the old class, whose qualifications are set out in Section 2 of Chapter 5; these will be known as Associates *honoris causa*. Entry to the new class of Associates, to be known as Associates (*tout court*), is limited to persons between 21 and 29 years of age: they will pay a small annual subscription of one pound and have access to the meetings of the Society and the Library and be entitled to receive the Proceedings. They shall not retain their Associateship longer than five years, nor after they attain the age of 30. The ordinary Associateship is designed to meet the needs of the younger biologists, whether professional or amateur, who are not normally in a position to apply for full Fellowship.

By these arrangements we hope to attract to the Society the young blood which it requires, and we hope also that the majority of the new Associates will, in due course, become full Fellows. At the same time, by retaining the class of Associates *honoris causa*, we continue the old and honourable tradition of the A.L.S.

The alterations in Chapter 8 are designed to bring the procedure of the election of Council into conformity with the Charters. Five members of Council must be removed annually, and balloting will take place to fill these five vacancies ; the Council will not be balloted for as a whole, as in previous years. Special provision is made in Section 2 for the nomination by Fellows of candidates for membership of the Council. This has always been a right of Fellows, but it is hoped that more advantage will now be taken of it under the new arrangements.

The question of Composition Fees is one which has given the Council some trouble and very great assistance has been given to it in this matter by Mr. D. M. Reid. The existing scale was fixed rather high and was not very attractive to prospective compounders. The Council felt that something should be done to meet the case of Fellows of long standing who, at the time of their retirement from professional posts, might find it difficult to continue paying the Annual Contribution indefinitely or to afford the Composition Fee laid down in the original scale. They accordingly proposed, and the Society approved, that Fellows of 20 years' standing or over who have reached the age of 65 may compound for the much reduced sum of £20, and may pay this in the form of five annual subscriptions.

As the membership of the Society has fallen well below its maximum of 800, it was considered inopportune, for financial reasons, to reduce the Composition Fee throughout the whole range. In happier times, when the membership has grown again, the question of reducing the Composition Fee may well be revived.

One other point regarding membership should be mentioned here. The Council has decided to adopt the principle of annual elections for Fellowship. Instead of having four ballots in the year, it is proposed now to have only one, to take place at the Anniversary Meeting. All Certificates of Recommendation received up to the 1st March each year will be carefully scrutinized by the Council and special attention paid to the published work of the Candidates in order that an adequate standard for the honour of Fellowship may be maintained.

The Sectional Committees to which I referred in my last review of the progress of the Society have continued to be active, and the first fruits of the work are coming to hand in the shape of lists or keys or materials for such. 'A Key to the British Opiliones, or Harvestmen', has been prepared by Mr. T. H. Savory, and it will in due course be published in the Society's Proceedings and reprinted in separate form as the first of a series to be known as 'The Linnean Society's Synopses of the British Fauna'. A list or Key to the British Caprellidae has been submitted for publication by Mr. R. J. Harrison, the first of our new Associates ; and others are in view. A great deal of work remains to be done in the detailed study of the British Fauna, especially in the neglected groups, and in this task both professional and amateur workers can give valuable assistance. Except for certain well-worked groups literature is

so scattered that even professional workers have considerable difficulty in identifying the species. It is in order to help in this task that we have started to publish, in small sections, a series of synopses of the British Fauna, dealing first with the groups that are little known. It is hoped that this undertaking will stimulate interest among professionals and amateurs alike, in the natural history of British animals. Let me recall the words of our Charter, which define the object of the Society as 'the Cultivation of the Science of Natural History in all its branches and more especially of the Natural History of Great Britain and Ireland'.

The Committee on Marine Algae has held most useful and successful meetings, and is now working out a scheme for the systematic collection of ecological data relating to the British forms, especially the Fucaceae. The Committee, which is under the energetic leadership of Dr. Delf, would welcome further members, both botanical and zoological, since there is need of team-work in the study of the inter-relationships of the littoral flora and fauna. It is hoped to establish liaison with the Marine Biological Association.

A new sectional Committee, suggested by Mr. C. C. Hentschel, will shortly be set up to consider standard nomenclature for the anatomical features of animals and plants commonly referred to in text-books.

With regard to the ordinary publications of the Society, we have kept within our restricted allotment of paper and, although printing is slow, satisfactory progress has been made with the publication of the Proceedings. We have received, through the Royal Society, a sum of £100 from the Government grant, which is being used to help publish the Journal. We are greatly indebted to the Rockefeller Foundation for a grant of £200 in aid of publication which will be used shortly in the production of a long and expensive paper which would otherwise be beyond the Society's means to publish. An Address list of Fellows and Associates was printed and distributed in September 1942.

Much hard work has been put in by a Sub-Committee of the Library Committee in preparing a catalogue of the Library on separate slips. This is a preliminary step towards the re-arrangement of the Library which is overdue and must be undertaken after the War. Provision will have to be made for much extra shelving and some considerable expense incurred for this purpose when conditions permit. The very valuable books of the Francis Druce Bequest are in the Society's possession, and a list will appear under the heading of Accessions to the Library in the next issue of the Proceedings. A reserve fund is being built up for use after the War to purchase books and journals not now available.

I referred at some length in my last account of the welfare of the Society to the great undertaking of the photographing of the Linnaean Collections and Manuscripts which was brought to so successful a conclusion with the help of a munificent contribution from the Carnegie Corporation of New York. An annotated catalogue of the completed films is now in preparation by the Assistant Secretary, and three sets of the positive films have been distributed, one to the University Library of Uppsala, the other two to the United States of America.

All the ordinary meetings of the Society have been held in conjunction with the Zoological Society of London, liaison being established through

the good offices of the Zoological Secretary. The auditory properties of the Meeting Room, which were much impaired as the result of a blitz and gave rise to justifiable complaint, have now been considerably improved through the action taken by the Ministry of Works in sound-proofing the windows.

The Society continues to be represented by its Secretaries at the Conference on Nature Preservation. A Memorandum on 'Nature Conservation in Great Britain' has recently been issued for the use of the Conference by the Society for the Promotion of Nature Reserves. Miss M. S. Campbell continues to represent us on the Phenological Committee of the Royal Meteorological Society.

In July last year we received a telegram of greeting from the Moscow Naturalists' Society, the oldest scientific society in the Soviet Union, in which they paid tribute to the memory of Charles Darwin, who was an honorary member of that Society. A suitable reply was sent, expressing the admiration felt in this country for the magnificent resistance of the Russian people to Nazi aggression.

In conclusion, as this is my last appearance as President, let me say how much I have enjoyed my tenure of office, and let me express to the Officers, the Council and the Staff my deep gratitude for the great help and kindness they have shown me throughout. These last three years have been a difficult time for the Society, but the worst is now over, and we may look forward with confidence to brighter days ahead, to a new revival and expansion of the Society's activities.

The Ballot was closed at the due time, and the result declared to the Meeting,—New Members of Council.—Dr. Margaret A. Brett, Mr. A. D. Cotton, O.B.E., Dr. P. W. Richards, Miss R. F. Shove and Mr. R. Winckworth.

(The retiring Councillors were Dr. E. Marion Delf, Dr. F. C. Fraser Prof. T. M. Harris, Prof. T. G. B. Osborn, and Dr. J. Ramsbottom, O.B.E.)

The President declared the Ballot for Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting,—Officers.—*President*: Mr. A. D. Cotton, O.B.E.; *Treasurer*: Colonel F. C. Stern, O.B.E., M.C.; *Deputy Treasurer*: Dr. B. Barnes: *Botanical Secretary*: Mr. I. Henry Burkill; *Zoological Secretary*: Dr. Malcolm A. Smith.

The President then delivered his Address, 'The Stereotypy of Instinctive Behaviour'. [Printed on p. 186.]

On its conclusion, Dr. J. Ramsbottom, O.B.E., addressing the President, said:—

I have been asked by the Secretaries to put a time-honoured motion to the meeting. Before doing this, Sir, I should like to express to you the heartfelt gratitude of the Fellows for the great services you have rendered to the Society during the past three abnormal years. Many in this room know—and the rest doubtless can guess—the labour entailed in presiding over our Society—a Society so rich in history and traditions—

even in normal times, and it cannot be said that recent years have been normal even in a Linnean sense.

When vacating the Chair on your election I expressed my confidence that the affairs of the Society were in good hands. I am afraid, Sir, that you have had a sticky wicket, but, to follow the phraseology of your Address, you have proved yourself capable of modifying your behaviour to meet abnormal situations—and for this, for your labours on our behalf, for your patience and cheerful spirit, we thank you. For myself I am indeed sorry that your Presidency has had more than its proper share of worries and anxieties with none of the lighter social alleviations, but I know that you will join in the hope that long before your newly elected successor reaches the prescribed 'allotted span' of office the glass will have set fair.

Dr. Ramsbottom then moved 'That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows'. The motion was seconded by Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., and being put to the meeting was carried with acclamation.

PRESIDENTIAL ADDRESS.

By E. S. Russell, O.B.E., M.A., D.Sc.

THE STEREOTYPY OF INSTINCTIVE BEHAVIOUR. With an Appendix on Valence as 'Meaning for Action'.

I return in this Address to a further study of the specialization of instinctive behaviour on the perceptual and the executive side which I dealt with in outline in my Address of 1941. This specialization brings with it an inevitable limitation of capacity both in perception and action. In conditions which are normal for it, and in relation to normal events and sequences, to which it is pre-disposed to attend, the animal will act, in its own way, in a manner that is biologically adequate. But in abnormal surroundings, or when faced with unusual events, the instinctive animal may be powerless to adapt its behaviour to the new situation, and may simply carry out its usual responses in a routine and stereotyped manner. Even in its natural environment it may be indifferent to biologically adequate objects or events if they occur outside the normal range of its specialized attention.

It is, for example, a well-established fact, though a remarkable one, that the valence of an object may depend upon its 'setting'; outside the environmental situation in which it is normally found or is normally sought for, its valence may be lost or transformed.

Here is a simple example. The larger dragonflies, such as *Aeschna*, capture their prey on the wing, as they patrol up and down in the air. According to Tirala (1923) they will chase anything that moves in the air in the same sort of way as their prey—a piece of paper or a leaf fluttering down, but not a ball of paper rapidly projected. It is the normal flying motion of the customary prey that attracts, or a passable

imitation of it. But the dragonfly will not attack even its normal prey crawling on the walls or bottom of the cage in which it is confined; in such a situation the prey loses its food-valence.

An even more striking case of food-valence depending upon movement within a particular environmental complex is afforded by the observations of Bierens de Haan (1929) on *Octopus vulgaris*. This cuttlefish feeds mainly on crustacea, and particularly on crabs, which it finds by observation of their slightest movements as they crawl along the bottom. Biernes de Haan made the curious discovery that a crab suspended in the water by a thread had no food-valence for the octopus, but was treated rather as an object having danger-valence. When the crab was moved quite near it, the octopus tried to blow it away by directing a stream of water towards it with its siphon. When the crab came in contact with the octopus and chanced to touch one of the suckers it was seized at once and carried to the mouth; through chemical sense its food-valence was again perceived. And when the hanging crab was lowered to the bottom and started to crawl thereon, it immediately acquired food-valence as a visual object, for the octopus leapt upon it at once.

It seems, then, that the perception that gives rise to the action of seizing as prey is of an object showing a particular mode of motion in a particular setting. The crab sprawling in mid-water has a different valence from the crab crawling on the bottom. 'Crab' as an individualized object, always recognizable as such, does not exist for the octopus. It appears with food-valence in the visual field only against the background of the environment *in which the octopus usually seeks it*. In another—unusual—situation it appears with a different valence; it is not for the octopus the same object all through. If it is completely motionless, it may have no valence, may not be perceived at all, save as part of the neutral background of action.

The proper explanation of these facts seems to be that the octopus is a specialized ground feeder—as the dragonfly is specialized to capture its food in the air. Being so highly specialized in this way, it is incapable of recognizing as food objects suspended or swimming in mid-water. Parallel examples may be found among fish. Thus the sole, which feels for its food in the sand by means of the cirri on the underside of its head, will pay no attention to a worm hanging above it, though it can see it perfectly well (Steven, 1930). And the dragonet (*Callionymus lyra*), according to the same observer which skims along within a centimetre of the bottom picking up its food, will completely ignore anything that may be swimming above it. Some other fish, on the contrary, such as bass, bream, dory and pollack, will take food swimming or sinking in the water, but will not touch the same food lying on the bottom (Bateson, 1889–90).

In all these cases the animal is specialized so highly that food objects have food-valence for it only in a particular environmental setting, that in which they normally occur and in which the animal is instinctively predisposed to seek them.

That a biologically significant object may lose or change its valence when it is removed from its normal spatial setting is well illustrated by

the behaviour of birds and fishes (and other animals) with respect to nests, eggs and young. There is here a good deal of evidence that the normal incubation-valence of eggs and young is linked rather closely with their being in the nest, and that outside the nest they may lose this valence entirely.

For example, Kirkman (1937) has shown for the black-headed gull that the valence of an egg may depend on its spatial relations to the nest. If an egg, its own or another's, is placed close outside the nest of a brooding bird, it will roll the egg back into the nest, placing the underside of its beak against the far side of the egg and rolling it in. 'Egg close to the nest' appears to have imperative valence, for the bird may roll an excessive number into the nest—up to seven in addition to an original clutch of two. This occurs even when it would seem that the brooding urge should be satisfied by a full clutch of three.

If the egg is placed 9 to 12 inches from the centre of the nest, some birds will roll it in, and some will not, if there are left one or two eggs in the nest. But if all the eggs are taken from the nest and placed outside at these distances, all the birds will roll at least one egg back into the nest. There is, therefore, a relation between presence or absence of eggs in the nest and the retrieving response.

When the eggs are placed still farther out—at $1\frac{1}{2}$ feet from the centre—the nest being left empty, the response varies. About half the birds experimented with rolled one or more eggs back into the nest; one sat on the eggs and built a nest round them; eight hesitated between rolling and sitting and achieved neither completely; four ignored the eggs completely, treating them as 'part of the landscape'.

The final experiment was to put the eggs out at 3 and 4 feet from the centre of the nest: the usual response was either to sit on the eggs, and build a nest round them, or to ignore them entirely. Thus the egg may lose its incubation-valence completely if it is removed a certain distance from the nest.

It is significant in this connection that other objects besides the egg have incubation-valence when placed in the nest, provided they are neither too small nor too large and have a certain roundness of contour, and that these objects may be rolled back into the nest if removed not too far away. There is, for the black-headed gull, no such object as 'an egg', recognizable as such in all circumstances; the incubation drive may be directed to any similar object in or close to the nest; normally, of course, the 'incubandum-in-nest' is an egg *.

Egg-retrieving is shown by other ground-nesting birds, such as terns and geese, whose eggs may be displaced from the nest by the movements of the incubating parent. In normal conditions, as Kirkman has observed, the black-headed gull when scared off the nest may roll an egg out of the nest so that it lies near by. Its instinctive make-up seems to be adjusted or adapted to dealing with this common accident by retrieving the egg, but not to tackling the more unusual case of an egg lying at some distance from the nest.

* A fuller account of Mr. Kirkman's remarkable experiments is given in an Appendix to this Address, pp. 201–208.

When the young cuckoo in the nest jerks its foster brothers overboard they sometimes lie close to the nest and in full view of the brooding parent, but she pays no attention to them—they have completely lost brooding-valence. A case of this kind is described by Hudson (1903) in his inimitable way. 'The young robin, when ejected, fell a distance of but five or six inches, and rested on a broad, bright green leaf, where it was an exceedingly conspicuous object; and when the mother robin was on the nest—and at this time she was on it the greater part of the time—warming that black-skinned toad-like spurious babe of hers, her bright intelligent eyes were looking full at the other one, just beneath her, which she had grown in her body and had hatched with her warmth, and was her very own. I watched her for hours; watched her when warming the cuckoo, when she left the nest and when she returned with food and warmed it again, and never once did she pay the least attention to the outcast lying there so close to her. There, on its green leaf, it remained, growing colder by degrees, hour after hour, motionless except when it lifted its head as if to receive food, then dropped it again, and then at intervals it twitched its body as if trying to move. During the evening even these slight motions ceased, though the feeblest flame of life was not yet extinguished; but in the morning it was dead and cold and stiff; and just above it, her bright eyes on it, the mother robin sat on the nest as before, warming her cuckoo' (p. 24). Other cases are referred to by Dewar (1928), where young birds fallen out of the nest are completely disregarded. The lack of attention to the ejected nestling may perhaps be due to its not exhibiting the 'begging' action, the raising of the head and gaping widely. According to Tinbergen (1938), if the nestling is replaced in the nest with the young cuckoo, it will not be fed until it warms up and begins to show the gaping action. These observations indicate that in the case considered the mother bird does not recognize her nestling as an object of specific size, shape and colour, but simply as something, *in the nest*, that gapes. It is a common experience that parent birds give most food to the nestlings that gape most vigorously, and neglect those that make more feeble demands, even allowing them to die.

The very fact that a small passerine bird will assiduously feed and tend the young cuckoo which she has hatched indicates that her instinctive behaviour is directed, not to her own young as specific objects, but merely to 'something in the nest that gapes'.

When the eggs of the stickleback (*Gasterosteus aculeatus*) are in their normal situation, that is, inside the nest, the male tends and guards the complex 'nest-with-eggs' in a characteristic and adaptive manner. Eggs that fall out he normally replaces in the nest. But according to Leiner (1929) eggs laid by the female in the open—an unusual occurrence—are not guarded by the male, and a batch of unfertilized eggs placed near a male guarding his nest was eaten by him.

Wunder (1930) and ter Pelkwijk and Tinbergen (1937) have also observed that eggs near the nest may be eaten instead of being replaced in the nest. It appears, therefore, that the valence of the eggs is dependent to some extent upon their spatial association with the nest; what is normally guarded is 'nest-with-eggs'. In the spider *Theridium*,

Montgomery (1906) observed that the eggs may be eaten if the egg-mass is broken up—what is guarded is the egg-mass as a whole.

Sometimes we find that an animal will not carry out its normal instinctive behaviour except when it itself is in its normal position or situation. This is so with the ant-lion, according to Bierens de Haan (1924), who has shown that if it is kept in a pill-box without sand it will not attempt to capture the ants with which it is supplied; it will treat them as enemies to be warded off, and not as prey, even when it is hungry. It seems that normal position at the bottom of its sand-funnel is necessary, and that insects have food-valence only when they come tumbling down the cone-trap, heralded by a fall of sand; also they must be pulled below the sand before the ant-lion will eat them. Normal position, and normal sequence of events are required to establish the adequate 'food-situation'.

One is reminded of the classical observation of Volkelt (1914) that, for a certain spider that lurks at the mouth of a tube leading from its web, a fly entangled at the entrance has enemy-valence and not food-valence, as it would have if caught in the web. I have dealt with this case in my previous book (1934, 1938) and need not further consider it here.

Herrick (1935) has shown that in the brown thrasher (*Toxostoma rufum*), the cowbird (*Molothrus ater*), the black-billed cuckoo (*Coccyzus erythrophthalmus*) and others, the 'begging' response of the nestlings can be elicited during the first few days whether the little bird is in the nest or not, but later it is given *only when in the nest*. Normal position in the nest becomes a necessary condition of the response. Of the cuckoo he writes: 'At first this food-response is mechanically given not only to hunger but to any stimulus of sound or touch, whether the bird is in its nest or out of it, and as often as the stimulus acts, it will be repeated within the limits of repletion or fatigue . . . . but from the second day onward it becomes more and more uncertain, especially when the bird is removed from the fragile platform of twigs which seems to answer well enough for a nest. At the age of one week, association with parent and nest has become so perfect that the young cuckoo when removed from its familiar twig "saucer" will starve rather than open its mouth' (p. 93).

Whether this is a phenomenon of association, as Herrick suggests, seems uncertain; it might well be due to maturation.

Many instinctive activities, such as, for example, the behaviour of a hunting wasp in seeking for prey, stowing it in a burrow, laying an egg on it and closing up the burrow, are carried out in a regular order or routine, and if this routine is upset the animal shows little power of altering its behaviour to meet the new situation. Also an object which has high valence at one stage of the process may have none at all when presented at a later stage. Here is an example from Hingston (1928), relating to the digger-wasp (*Psammophila tydei*). After she had dug and provisioned her burrow with a caterpillar on which she laid an egg, and was engaged in closing the burrow with small pebbles and bits of slate, Hingston broke open the tunnel and extracted the caterpillar with egg attached. He laid it down right across the entrance to the

tunnel. When the wasp returned she paid not the faintest attention to the caterpillar, but went on with the work of filling up the tunnel in the normal way. The caterpillar was, therefore, valent as 'something to be placed in the burrow' only at the appropriate stage in the action-sequence.

Further examples of this phenomenon will be found in Bierens de Haan (1940, pp. 228–232).

The rigidity of instinctive routine is such a well-known phenomenon that it is unnecessary to illustrate it in great detail. Here are a few examples showing how difficult it is for the instinctive animal to break away from its stereotyped behaviour and to adapt itself to unusual conditions or unusual events.

First some very simple cases. M. Tweeddale (1936) relates that some baby badgers which she reared never tailed after her, but kept between her feet as she walked; the explanation is that in normal circumstances they keep station under the body of the mother when she moves about. The normal response of the skunk to approaching danger is to stand firm and attempt to frighten the enemy away; this stereotyped method is used, with disastrous results, when the skunk is confronted with a fast-moving car—hence the heavy mortality of skunks upon American motor roads (Abbott, 1939).

The behaviour of young nidifugous birds, such as terns, plovers, pheasants, oyster-catchers and many others, in crouching motionless at the danger-call of their parents is very effective in hiding them from their enemies, especially as they are for the most part protectively coloured. But this instinctive behaviour, admirably adapted to normal circumstances, will be carried out unchanged in conditions in which it is perfectly useless; 'they will crouch just as readily on a lawn or a carpet, against which they are conspicuous in the extreme' (Huxley, 1930, p. 86). Young terns and young lapwings, placed upside down, so that their white under-surface shows up clearly, will remain rigid and motionless just as if they were right side up (Tomlinson, 1930).

I have referred in my 'Behaviour of Animals' to the case of the mason-wasp (*Sceliphron*), which normally builds on the bark of a tree and camouflages her nest elaborately, so that it blends with its surroundings; on a mantelpiece she carried out the same routine of decoration, thus rendering the nest particularly conspicuous. A parallel may be found in the behaviour of the trapdoor spiders (*Nemesia*), studied by Moggridge (1873) on the Riviera. These conceal the door of their trap by weaving into it moss and other vegetable material found in the vicinity, and normally this is effective. But they will decorate the door in the same way even if there is a patch of bare earth surrounding it, thus rendering it conspicuous. 'In one case', writes Moggridge, 'where I had cut out a little clod of mossy earth . . . containing the top of the tube and the moss-covered door of *N. caementaria*, I found, on revisiting the place six days later, that a new door had been made, and that the spider had mounted up to fetch moss from the undisturbed bank above, planting it in the earth which formed the crown of the door. Here the moss actually called the eye to the trap, which lay in the little plain of brown earth made by my digging' (p. 120).

The Californian woodpecker, which has been very fully studied by Ritter (1938), is known to store large quantities of acorns, digging little pits in the bark of certain trees and ramming the acorns in. Sometimes it utilizes the natural fissures in the bark. The action is instinctive and is often carried out to excess, far more being stored than are ever used. Also in British Honduras, where there is no need for storage of acorns against times of shortage, the local race of the species carries out the same instinctive routine.

Normally, when only trees are available, the storing goes on quite happily—though by a curious aberration pebbles and stones are occasionally stored as well as acorns—but when the bird encounters and uses objects of human construction, such as houses and telegraph poles, trouble may arise and the storing become quite ineffective. Ritter records that the birds are fond of using the dry-weather cracks in the telegraph poles, which they stuff full of acorns, saving themselves the trouble of digging out holes, but when the wet weather comes and the wood swells the cracks contract and squash the acorns to pulp.

The woodpeckers may also be led astray when they attempt to store acorns in the walls of wooden sheds or houses. It is quite usual for them to drill holes in such situations, right through the walls or window-casings, and insert their acorns, which naturally fall through, and are lost for ever. Ritter gives a lively description of such a case. In an old miner's cabin in the Californian woods 'the box window and door casings and the board sidings generally presented an example of the hole-drilling industry of woodpeckers that, once looked upon, could never be forgotten by anybody. As for the acorn storing, since all the holes went clear through the boards, virtually none of the acorns put into them stopped there, but all fell down on the other side—somewhere'. He estimated that over 60,000 acorns had been thus pushed through into the hut—stored where the birds could not get at them.

This sounds like gross stupidity on the part of the birds. Actually it is hardly that. It is something much simpler. It is merely the application of a routine instinctive activity in circumstances or conditions of an abnormal kind, to which the activity is not adapted. Telegraph poles and houses are not the usual or historic environment of the woodpecker. They are in some respects the functional equivalent of trees and are utilized by the bird as such, but they are not so well adapted for the purpose as trees.

Instinctive activity fits, or is adapted to, normal circumstances or environment; when the unusual is encountered, to which it is not adapted, it is apt to fail. The usual routine activity is carried out, but it may not reach its mark in unusual conditions.

In most species of pigeon, according to Lorenz (1935), the female sits on the nest from late afternoon till the next forenoon, the male relieving her during the rest of the day. This routine seems to be ingrained in the male at least, as the following observation shows, which I take from Lorenz (p. 343). A pair of house pigeons had hatched out their nestlings when the female fell a victim to a cat. The male carried out his routine duties of incubation during the normal period, and shortly after the hour when he would have been relieved by the female he went

off to feed. In the evening he took up his usual sleeping perch near the nest, and did not brood the callow young. As the night was cold the nestlings perished. In the morning, about ten, the male settled down on the nest and brooded the little corpses till late in the afternoon. He kept up this senseless routine for two days.

Some similar cases have been collected by Dewar (1928) from the experience of aviculturists. An exact parallel to Lorenz's observation is provided by Mr. B. Aitken, whose account is quoted by Dewar (p. 115). A bereaved male pigeon was left with a nestling not more than a week old. He made no change in his incubation period, sitting on the nest only from about ten till two during the day, leaving the nest exposed all night while he slept elsewhere. In spite of this treatment the little bird survived. A male saffron finch (*Sycalis minor*) observed by Dr. Amsler, when bereaved of his mate, reared his young successfully, although he brooded them only by day, his normal period.

In a species of sand-grouse (*Pteroclurus exustus*) observed by Mr. St. Quintin, the hen incubates by day, the cock by night. In his aviary there were a cock and two hens, and one year both hens laid at the same time. Each sat on her eggs during the day, but made no attempt to incubate at night. The cock sat by night, sometimes in one nest, sometimes in the other, but the eggs got chilled (Dewar, p. 35).

In these cases behaviour which was adequate to the normal situation was continued without modification in an unusual situation ; the change in conditions was, in effect, not perceived or attended to. The rhythm of action proved too strong to break.

In raptorial birds it is usual for the male to capture food for the young and bring it to the nest plucked or skinned ; the female then picks it to pieces and feeds it to the young (Dewar, 1928, p. 123). If the female is killed and the male does not find another mate, he carries on with his part of the work, but does not take on the female's share, with the result that the young die, if they are not of an age to feed themselves. Mr. J. H. Owen is quoted by Dewar as having observed this happening to a young brood of sparrow-hawks (*Accipiter nisus*), whose mother was killed when they were about a fortnight old and unable to feed themselves. ' When we examined the nest a day or two later ', writes Owen, ' we found all the young dead and a pile of six dressed finches and buntings on the edge of the nest '. As Dewar says, ' Here we have proof that feeding the young is a purely instinctive operation, of which the parents do not appreciate the significance. Instinct causes the male sparrow-hawk to bring to the nest quarry dressed and ready to be torn up. Here his job ends. If the female is not there to complete the work, the young starve if they are not old enough to tear off flesh '. Thus behaviour which is adequate in normal circumstances is incapable of modification to meet an unusual situation.

An interesting observation by Bickerton (1927) shows that the feeding of the young in the nest may be a stereotyped activity, independent of the number of young present. He watched regularly a nest of the mistle-thrush (*Turdus viscivorus*) in which four eggs had been laid, only one of which hatched. He removed the three infertile eggs. He noticed that the parents brought such ample supplies of food that the solitary

fledgling could not cope with them, and lay inert and irresponsive through a surfeit. Further observation showed him that the parents were bringing every day as much food as was required for four or five nestlings —the normal number to be supplied. The routine was followed, without adjustment to the changed situation—which was not, in practice, perceived.

Very specialized adaptive behaviour is shown by the male sand-grouse (*Pterocles*) in providing water for his young. The birds nest in the desert, often a long way from water: the male flies to a source of supply and saturates his breast and belly feathers, and when he returns the young suck the water from him. It has been observed by Meade Waldo that the whole elaborate routine may be gone through in an aviary, where a much simpler procedure would suffice. The male rubs his breast up and down on the ground until the feathers are awry, then saturates them in the drinking water. 'When soaked he goes through the motion of flying away, nodding his head, etc.; then, remembering his family is close by, he would run to the hen, make a demonstration, when the young run out, get under him, and suck the water from his breast—the appearance being that of a mammal suckling her young. The young pass the feathers through their bills, and keep changing places until the supply becomes exhausted. Until the young can fly *they take water in no other way*, and the cock gives it to the young only'. (Quoted by Buxton, 1923.)

Routine and stereotyped behaviour is often shown by nestlings. Here are two examples. It is a usual habit of young birds to defaecate over the edge of the nest. In the noddy tern (*Anous stolidus*) the typical behaviour will be carried out even when the bird is removed from the nest. 'When defaecation becomes necessary the bird backs quickly to the rim of the nest, stops suddenly, and forces the fecal matter far out over the rim (sometimes 8 to 10 inches). The birds in captivity, even when on a perfectly smooth floor, held to the same habits of defaecation'. (Watson, 1908, p. 240.)

The observations of Dewar (1921) on the creeping back to the nest by very young nestlings of the willow warbler (*Phylloscopus trochilus*) indicate that this is an instinctive action adjusted to the normal contingency, and not adaptable to unusual conditions; the instinct is simply to turn round and move forwards, and this normally brings it back to the nest; but if it is placed facing the nest it will turn and move away. 'The chicks', writes Dewar, 'had their eyelids closed. One was placed a foot from and with its head directed away from the nest; it turned round and crawled back into the nest. A second was placed 6 inches from the nest with its head turned away from the nest: it also turned and crawled towards the nest. A third was placed a foot from and with its head directed towards the nest; it turned round through an angle of about 130° and crawled farther away from the nest. A fourth was placed 3 inches from the nest with its head directed towards the nest; it turned through an angle of 45° away from the nest and went past the nest for 6 inches. A fifth was placed directly in front of and looking into the nest; it turned round through an angle of rather less than 180° and moved away from the nest" (p. 105).

There are a number of observations on birds which indicate how easily they drop into a habitual routine—not purely instinctive, because based on habit, but representing probably a falling back into the almost somnambulistic routine characteristic of instinctive behaviour. When a bird's nest is removed a short distance away from its original site, it is very usual for the parents to hover over the spot where the nest first stood, and to disregard for a time the nest in its new situation. Here are some observations by Watson (1908) on the sooty tern (*Sterna fuliginosa*) which illustrate this clearly. Finding a nest in the sand close to a conspicuous tuft of grass, he obliterated it and made a new nest 88 cm. distant, planting the tuft of grass in the same position relative to the nest. In spite of this displacement of the landmark the bird, on returning, stood for 8 minutes at the old site, 'then put down its beak and attempted to arrange the egg just as though it were present'. It alternated between the old and the new site, and on several later occasions settled down first at the old site. Three other birds showed similar behaviour.

An even more striking experiment was the following. He placed a nest in a pan and raised it on stakes one metre high; the bird found it immediately. Later he moved the nest one metre away, still on the stakes: the bird on returning hovered in space many times just at the spot where the nest had been, and attempted to adjust to the nest that was not there; finally it alighted on the displaced nest.

Many examples are given by Herrick (1901, 1935) of the same sort of behaviour. Here is one of them. The nest of a kingbird (*Tyrannus tyrannus*), together with the branch on which it was built, was removed to another position 20 feet away. Both birds began to explore the original tree; they would 'fly to that point in space which the nest formerly occupied, and hover over it repeatedly, a characteristic action of many birds under such circumstances' (1901, p. 22). Herrick also records that many birds when approaching the nest do so always in the same way, following exactly the same course each time.

This curiously stereotyped behaviour in approaching the nest and in seeking it in its original position has been very fully and carefully described by Elliot Howard (1929), as follows:—

'A yellow bunting flying round with dead vegetation in her beak is attracted by a bramble bush covered with honeysuckle. She must enter it to lay the foundation of her nest, and there are a number of ways by which she can do so; she must choose one; or enter here, enter there at haphazard—so at least one would imagine. She does neither. To begin with, she has three ways of entering and leaving the thicket—a front entrance, a side entrance, and a back entrance. On May 12th, while I watch, she goes in at the front and out at the back nineteen times; in at the front and out at the side six times; in and out at the back once. On May 13th she discards the back and side entrances, entering at the front and leaving at the back each time. Afterwards she makes the front entrance the sole pathway to the nest. When the young are hatched I cut away the leaves and brambles and expose the nest. She comes with food, sees nest and young in full view through my opening, approaches and hops to and fro with neck strained towards

them. But though within a few inches of them she cannot feed, though they stretch their necks she cannot alter her routine; and so, stupid as it may seem, she has to return to the opposite side of the thicket and enter by the usual path—coming back to the very position from which she started—before delivering the food she carries' (p. 106).

Further observations by Elliot Howard on the yellow bunting (*Emberiza citrinella*) indicate that if the nest with young is moved a few inches away the original site still retains a strong attraction for the female. If the nest is replaced, but the young removed to another nest alongside, the original nest, though empty, is still highly attractive. 'She broods the empty nest and tries to get comfortable on nothing; then returns to the young and tries to brood but cannot, and so runs to and fro, brooding the young and the empty nest alternately; and on the empty nest she bends her head, fluffs out her feathers, and works her legs as if the young were beneath her' (p. 54).

In addition to showing the power of routine, these observations by Watson, Herrick and Elliot Howard also illustrate a very striking fact about instinctive behaviour, namely, that it may be carried out in symbolic fashion even in the absence of the appropriate object to which it is normally directed; it seems that the hormic impulsion to carry out certain acts is strong enough to set them going in inappropriate conditions; they seem to some extent independent of the perceptual situation.

We see something of the same kind when an animal carries out an instinctive routine of behaviour in an environment which is quite different from the normal environment to which the behaviour is pre-adapted. Take, for instance, the burying behaviour of the dog and other animals (Russell, 1937).

Most dogs bury, or try to bury, in the ground, bones and other surplus food. There is evidence that this behaviour-mode is, to begin with, purely instinctive. It appears fairly late in puppyhood, somewhere about the fourth month or later, when the pup is completely weaned, is well fed, and is experimenting with all sorts of objects, edible and inedible. Miss Pitt (1927) has observed its spontaneous appearance in a fox cub reared in isolation, and it is highly unlikely that it arises in dogs through imitation of their elders.

The action of burying is curiously stereotyped and invariable. When carried out in the open, in natural surroundings, in soft earth or sand, it consists in the scratching of a hole with the fore-feet, the placing of the bone in the hole, and the nosing of the earth over the bone, by a series of strokes radially directed towards the hole.

The objects buried are, normally, bones and other food objects which are not wanted at the moment. It is improbable that a young dog buries surplus food with the express purpose of digging it up later—the action is impulsive or instinctive rather than intelligent, at least to begin with. Later on, however, the action seems to become intelligent or consciously purposive for some dogs, at least, go to considerable trouble to bury their bones secretly, and they certainly remember where the bones are buried, and dig them up again.

But the interesting thing is that many dogs carry out this burying

action, and especially the second part of it, indoors, in the unnatural surroundings of the home. They will bury objects in a chair, on a bed, on the hearth, pushing them into a crevice and carrying out the typical sweeping motions with the nose, pushing, as it were, imaginary earth over them. This typical instinctive action, which is adapted to the normal circumstances of out of doors, is carried out, unchanged, in conditions to which it is not adapted.

Incidentally, I have noticed in one of my dogs a very interesting extension or development of the action of burying. She will bury symbolically, with the typical nosing action, not only surplus food, but also other objects lying in her bed or on her chair, such as her collar, cigarette ends or match stubs. The functional formula 'not wanted now', which applies to food objects, has been extended to cover objects 'not wanted here'.

Several other carnivores, and especially the foxes, bury their food in the same way that dogs do, and the habit is widespread among rodents also, though the manner of burying is different.

Squirrels, as is well known, bury quantities of nuts in the autumn, digging little holes in the ground, placing a nut therein and covering it up by scratching earth over it with their paws. They also will carry out this instinctive routine unchanged in the abnormal conditions afforded by a human habitation. There is a classical description of this in Lloyd Morgan's book 'Habit and Instinct' (1896), quoted from an American observer, C. F. Batchelder. He brought up indoors two young grey squirrels taken from the nest at a very early stage. 'These squirrels', he writes, 'were often taken from their cage for hours at a time, and given the freedom of a room. Here they got abundant exercise, climbing and jumping over the furniture, racing up the window-curtains, and leading, as well as they could, well-regulated squirrel lives. It was here, when they were a month or two old, that they first displayed a very interesting instinct. Many a time I saw one or the other of them take a nut, when there were more than he could eat, look about the room until he found a suitable place, then put the nut down on the carpet in some sheltered corner, such as against the castor of a sofa leg, or in the corner of the carved foot of a bureau. He would press the nut down on the carpet, and then go through all the motions of patting the earth over it, after which he went about his business as if that nut were safely buried . . . . the young squirrels were satisfied to bury their nuts in the nearest approach to a hole that they could find on the carpet, and were not disturbed by the fact that when the process was completed the nut still remained plainly visible' (p. 123).

The examples of 'symbolic' action illustrate a fundamental characteristic of instinctive behaviour, namely, that it is hormic or impulsive—'triebartig' or 'triebmässig', to use the expressive German words. While it is directive towards a normal end-state, and stereotyped in the manner of its carrying out, it is not, like voluntary action, determined by clear foresight of the goal; it is determined *a tergo*, by specialized impulse; it results from an inborn impulse to carry out certain acts in a certain way, in a particular situation. And the impulse may be so strong, and the mode of action so stereotyped, that the action may be

carried out in typical fashion even in a situation which is not normal or usual, and sometimes even in the absence of the appropriate object to which the action is normally related ; in such a case the action becomes, one might say, symbolic, and does not reach its normal biological end.

The hormic nature of instinctive behaviour—its partial independence of the perceptual situation—is clearly seen when we consider it on its first appearance in the life of the animal, when it arises, as it were, spontaneously, through the maturation of structure and function.

The shrikes (*Lanius*) have the peculiar instinct of impaling their food on thorns and other holdfasts, so that they may pick it to pieces and eat it. The action is, to begin with, purely instinctive ; it arises early in life, and in captivity may be carried out in the absence of thorns or their equivalents, as the observations of Miller (1931) and Lorenz (1935) have shown. Here is Miller's account of the first attempts at impaling carried out by the Californian shrike (*Lanius ludovicianus*). ' The first attempts at impaling have been noted in cage birds at the age of forty days. These attempts consist of dragging the food along the perches with a jerking motion, the head held low and the long axis of the bill paralleling the perch. If nails are provided in the perches, the food on encountering these obstacles offers resistance to the bird, which continues to tug, and may, on occasion, thus firmly lodge the food on the nails. Subsequently, small bits are picked from the impaled mass, first gently, but later they are torn loose with great vigour. If the food becomes dislodged from the nails, impaling efforts are renewed at the location of the former successful impaling. If nails are not provided, the first efforts at dragging food along the perch being unsuccessful, juveniles attempt to wedge their food into corners or between the wires of the cage. This is done always by pulling objects over or through crevices, and not by pounding them into such places ' (p. 214). The form of this behaviour-mode is fixed and constant.

Miller's observations are confirmed for the European species, *Lanius collurio*, by Lorenz. The young bird carries out the motions of impaling anywhere in its cage, whether thorns or nails are present or not. It seems at first to pay no attention to such holdfasts if they are present, but if the food catches on one of these projections the action is completed, the food is pecked to pieces. Thereafter thorns and functionally equivalent objects have significance or valence, and are sought out and used for impaling purposes. Apparently in this species the valence of thorns is not inborn, but rapidly acquired. However this may be, it is clear that the action arises as a pure ritual, which is carried out in typical form, though the conditions for its successful completion are absent. It is adapted to the normal—for in Nature a young shrike will find plenty of holdfasts—and is carried out unchanged in an inadequate environment. The action is at first carried out symbolically, as a ' Leerlaufreaktion ', to use Lorenz's term.

Lorenz (1937, 1938) lays perhaps exaggerated stress upon this characteristic of instinctive behaviour ; he regards pure instinctive behaviour as being essentially independent of perception, taking place in a stereotyped manner, as a fixed behaviour-mode or ' Bewegungsnorm '. The adjustment of the instinctive action to the particular situation comes

about, in his view, through orientating reactions, which are of the nature of taxis. Thus, in the egg-rolling response of the goose to an egg which has slipped out of the nest, he distinguishes (Lorenz and Tinbergen, 1938) two factors—the pure instinctive action of placing the beak behind the egg and bending the neck so that the egg is moved towards the nest, and the adjustment of the action by sideward movements of the beak to counteract the sideways slipping of the egg. The instinctive action is seen in its purity when it is carried out as a ' Leerlaufreaktion ', as may happen when the egg has dropped out of its reach, or when, confronted by an artificial egg of large dimensions, it carries out (in vain) the egg-rolling action in its normal amplitude. To my mind this rigid distinction between pure instinctive action and orientating movements is a nominal and artificial one, but Lorenz is certainly right in emphasizing the internal drive behind instinctive behaviour and its *partial* independence of the perceptual situation—in other words, its hormic nature. That the independence of perception is only partial is apparent from the fact that the young shrike carries out its first efforts at impaling only with food objects, and that the goose exhibits the egg-rolling response only with reference to an egg or egg-substitute out of the nest.

So, too, young birds may make their first attempts at bathing without entering the water at all, but they normally do so only in the presence of water. Here are some observations on the subject.

Lloyd Morgan (1896) tells us how, when he placed a pan of water in the cage containing some young jays (*Garrulus glandarius*) about three weeks old, they paid at first no attention to it. But when one hopped into it, probably by chance, it squatted and fluttered its feathers as if taking a bath, though its breast scarcely touched the water. Another, having pecked at the pan and wetted its beak went, through the motions of bathing outside the pan. A magpie (*Pica pica*), five weeks old, observed by Mr. H. T. Charbonnier behaved in a similar manner ; when supplied with a pan of water it made one or two pecks at the shining surface, ' and then, outside the pan, without entering the water at all, proceeded to go through all the gestures of a bird bathing, ducking its head, fluttering its wings and tail, squatting down, and spreading itself out on the ground ' (Lloyd Morgan, 1896, p. 97). Bathing as a ' Leerlaufreaktion ' in the presence of water has also been noted by Miss Tyrrell (n.d.) in baby tits (*Parus*) which went through all the motions of bathing on the grass near a saucer of water : ' the babies ducked and quivered their wings, and bent up and down, and quirked imaginary drops of water over their little backs ' (p. 107). My runner ducks go through all the motions of bathing, pouring imaginary water over their neck and back, but they do it usually when standing over depressions or holes in the ground, which might, but do not, contain water, or when rain is falling—in a ' water situation ', therefore, though standing water is not actually present.

In these cases, the impulse to bathe is released by the sight or touch of water, though it may be carried out in the air, as a symbolic action, in a quite typical manner.

To sum up, inborn impulse to carry out a specific mode of action is the fundamental thing in instinctive behaviour ; it arises generally in a

particular perceptual situation, but it may not be closely dependent on such situation. The impulse is not, as a rule, guided by foresight, and action is apt to be inadaptable to the unusual.

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APPENDIX.

Valence as 'Meaning for Action'.[1]

As a result of many years' intimate study, in the field, of the breeding behaviour of the black-headed gull (*Larus ridibundus*), the ornithologist F. B. Kirkman has provided a wealth of facts which are of the utmost significance for the theory of animal perception. These are published in his book of 1937, and in a series of subsequent short reports (1938, 1940, 1941), from which I summarize the following account of the perception-action relations between the breeding gull and its eggs or egg-substitutes. I have often had the privilege of discussing his results with Mr. Kirkman, and he has greatly helped me in preparing this account, though he is not, of course, committed to the interpretations here put forward. His very complete and accurate observations well demonstrate the value of the concepts of valence and equi-valence which I have outlined in previous publications (1935, 1936, 1938); they demonstrate also the complete inadequacy of any simple stimulus-response theory of animal behaviour.

When the nest is made and an egg laid in it the gulls start incubation, both sexes taking part. 'Brooding spots' have developed on the underside—three areas from which the feathers have moulted, and into which the normal clutch of three eggs is fitted when the bird settles down to brood.

The necessary conditions for incubation are (1) the psycho-physiological state of 'broodiness', a state of tension issuing in a drive towards incubation, and (2) the presence of at least one egg or egg-substitute in the nest, or nest-equivalent.

If the eggs are removed from the nest the bird settles down for a short time, but soon becomes restless and, finding something lacking, works off its incubation drive in various substitute actions, such as preening or adding material to the nest. If the eggs are not restored, the gulls desert within a day or two.

Kirkman found that a very wide range of objects would satisfy the incubating drive; such objects are accordingly functionally equivalent to the bird's own eggs; they included eggs of the species painted in bright colours, duck's eggs, pot eggs (as used by poultry-keepers), wooden eggs, plain or coloured, small wooden blocks with well rounded contours, various tin boxes and balls, if not too large, also a ball of camphor and a small lump of coal. Some of these objects were rejected by certain birds, but each was accepted by one or more individuals. Certain other objects, however, were not incubated by any bird, notably wooden blocks with only slightly trimmed edges, and smallish objects such as a watch and a small cotton reel, which sank down through the nest material and so did not come into contact with the brooding spots.

For the nest itself there could be substituted a tin plate and even a felt hat—anything, in fact, that kept the eggs together, and was thus functionally equivalent to a nest.

Kirkman summarizes his results, to 1937, as follows: 'As far as the black-backed gull is concerned, the conclusion may be stated provisionally thus: a complete normal incubating reaction will result from the presence

of two conditions, both of which are indispensable, namely, an internal drive or urge to brood together with an external situation in the form of an effective nest or nest substitute containing at least one egg or a substitute for that egg, the substitute being of any colour, shape, size, material, or smell, provided that its shape does not cause discomfort, that it is not too large to sit upon, or is not so small that it sinks into the material of the nest' (1937, p. 98). Later Kirkman (1941) found that a certain hardness of surface is a usual condition of acceptability as an egg-substitute.

The main valent qualities common to all acceptable egg-substitutes are, however, (1) a certain size, and (2) a clearly marked three-dimensional shape, preferably oval or round, with smooth contours. The incubation drive or need is satisfied by contact of the brooding spots with any object possessing such qualities.

These qualities are perceived tactually. A slight change in roundness of contour may make all the difference between comfort and discomfort, between acceptance for brooding and rejection; for instance, eight pairs refused to sit for any length of time on small wooden blocks whose edges had been slightly trimmed, but the same blocks with the ends cut away still more were readily accepted (see Kirkman's fig. iv, p. 95). Size is a very important factor, as the following experiments show. A gilt tin box, measuring 3 in. by 2 in. by 1 in., was rejected by two pairs, but accepted by a third: it was too large to be fitted into a brooding spot, but it is to be presumed that a corner of it satisfied the contact need. One pair tried to incubate a leather-covered ball 3 inches in diameter, but were unable to tuck it in beneath them, and soon gave up; smaller balls were readily incubated, especially golf balls. Objects, such as a silver watch and a small cotton reel, which owing to their small size sank into the nest and so made no contact with the brooding spots were abandoned. Larger cotton reels with their raised edges cut off were very readily accepted.

Later experiments on the range of equivalence showed that some gulls would accept for brooding an oblong tablet of soap, an egg-shaped object made of cloth, but not one made of tissue paper, and would reject an open pine cone and an empty cartridge case.

The first acquaintance with the egg-substitute objects is, of course, made by visual perception, and while the birds appeared to take no notice of what would appear to us as startling differences in colour (p. 90), there is clear evidence that they perceived differences between the substitute-objects and the normal egg. Thus ducks' eggs, which are much larger than the gull's, and pot eggs, which are shining white, excited alarm at first, though they were soon accepted.

The course of events may be formulated as follows. If the gull is intent on brooding, any visual object in the nest, or in a functional substitute for the nest, will excite attention. Normally this object is one of its eggs, and it will be treated as 'something to be incubated', i.e., fitted into one of the brooding spots. Other objects in the same situation, though their difference in appearance from the normal egg may be noticed, are, or may be, provisionally treated in the same way as eggs. If they are not too large, are fairly resistent, and have no sharp edges or points, they will be brooded, as functionally equivalent to eggs,

presumably because they satisfy the contact-need experienced in the brooding spots; if this need is not adequately satisfied the object will be abandoned. The visual characteristics of the object are not decisive factors in the behaviour, whether the object is an egg or an egg-substitute; what decide brooding or not-brooding are the size and contour qualities of the object, as perceived tactually *in relation to contact-need*. Given the incubation drive, the essential factors in the behaviour, as so far described, are (1) the object perceived *as being in the nest*, and (2) its adequacy or inadequacy as satisfying the contact-need of the brooding spots. (The satisfaction of this need is a necessary step or stage in the psychobiological process of reproduction; it is a goal subordinate and contributory to the biological end of the reproduction of the species, though the gull is entirely unaware of its biological purpose.)

In passing we may note that many other cases have been recorded of birds brooding biologically inadequate objects in place of their own eggs. Kirkman relates that gannets accepted white or highly coloured pot eggs and also a gilt tin box. Here are two cases reported in *The Field*:—

C. M. Clark notes (issue of 9 December 1936, p. 621) that in the nest of the oyster-catcher there is sometimes found a large pebble as well as a clutch of two or three eggs. One nest containing two eggs had in addition two balls of hard dried mud, which the birds turned as carefully as the real eggs when they settled down to brood.

From a hen which had nested out under a tree, all the eggs were taken away. She gathered fallen apples from some distance away, raked them into the nest and brooded them (G. H. Hewison, 21 October 1933, p. 1039).

Broody domestic hens, deprived of their eggs, will sit on almost anything remotely resembling an egg, or even on nothing. 'Link witnessed a barn-door hen sitting on some large flint stones. Von König-Warthausen saw a turkey covering potatoes. Mr. Blaauw tells of a Manchurian crane in his aviary which sat on a piece of brick it had fished out of its pond. Colonel Cunningham relates how an Indian kite (*Milvus govinda*) sat for many days on a pill-box it had abstracted from the room of a hypochondriacal member of the United Services Club, Calcutta' (Dewar, 1928, p. 30). 'Link records that a turkey, after her eggs were taken, sat on a growing turnip; when this was rooted up, she continued to sit for two days over the hole left by the uprooting' (*ibid.*, p. 38). Other cases are given by Dewar in his exhaustive chapter 'Strange eggs in the nest'.

Many experiments have been made in substituting for one or more eggs those of a different species. There is evidence that in some cases the birds perceive the difference and turn the strange eggs out at once or after a short period, or even desert the nest.

Discrimination against egg-substitutes appears to be usual in canaries. Miss Smith (Mrs. F. C. Bartlett) (1923) relates that 'she has more than once had hen canaries who would sit on clay eggs until their own were laid, whereupon they invariably proceeded to turn the clay eggs (and those only) out of the nest' (p. 86). Similar observations have been communicated to me by Mr. J. L. Bowen of Port Sunlight. After a canary had laid two eggs these were removed and two acorns substituted; after some time the canary ejected them and laid two more eggs; again the eggs were removed and replaced by acorns, which were later ejected and eggs laid, 'and so the cycle was repeated several times'.

Levick's observations on penguins (1914), which when deprived of their eggs tried to incubate pieces of ice instead, seem to indicate that the acceptance of strange and unsuitable substitutes for eggs is due to the strength of the incubating drive when baulked of its normal satisfaction.

Returning now to the gull, we note that an egg or suitable egg-substitute in the nest is essentially 'something to be brooded'; that is its *functional valence* or 'meaning for action'. But Kirkman has shown by an array of ingenious experiments that in certain circumstances an

egg and egg-substitute may have another kind of functional valence, being ' something to be retrieved '. In other circumstances still, an egg or egg-substitute may have no special valence at all, sharing with the rest of the landscape the general functional quality of solidity and resistance, and having at most obstacle-valence. To complete the tale of change of valence of an identical object, the egg, it should be mentioned that a gull's own egg even in the nest, if it has a large hole in it (made, for instance, by a predatory neighbour), may acquire food-valence and be eaten by its owner (Kirkman, 1937, pp. 49, 50, 154). Eggs, whether in or near the nest, have also ' to be guarded ' valence ; marauders must be kept away from them. Curiously enough, the same egg, in proximity to the nest, if damaged, may be treated alternately in quick succession as a food-object or as something to be guarded. Such a case is described in detail by Kirkman. An egg lying 2 feet from the centre of the nest was vigorously defended by the gull against the attacks of first a pair of jackdaws and then a marauding gull—which finally succeeded in breaching the egg but was then driven off by the owner gull. ' On returning from the chase, the nesting bird halted by the egg, now with a gaping hole in its upper side, and sucked it nearly clean. That was not the end. The bird continued to make vicious assaults upon any neighbours venturing to approach and investigate. After one of these assaults it paid another visit to the shell and cleaned it out meticulously. Nevertheless, it continued to drive off the inquisitive just as if the egg were still whole ' (p. 50).

Even an egg-substitute, namely a wooden egg of the same size and shape, may be treated as potential food by a marauder, being pecked or stolen (p. 94).

According to circumstances, then, the same perceptual object, an egg, may be treated *by its owner* as ' something to be brooded ', ' something to be retrieved ', ' something to be guarded ', or, if damaged, ' something to be eaten ' ; it may also cease to have any special functional valence at all. There is, clearly, no simple stimulus-response relation involved, nor is mere visual pattern or ' Gestalt ' decisive for the behaviour shown ; functional valence or meaning for action comes into the picture all through.

A striking example of the instantaneous change in valence of one and the same object is afforded by Kirkman's observations on the behaviour of a gull towards a piece of cake, which I shall quote in full.

Small cakes or fragments of cake about the size of an egg were usually eaten, when placed near the nest. ' Finally, however,' writes Kirkman, ' I had the satisfaction of seeing the selected bird back on its nest, a cake still intact just outside. The bird looked at the cake, and set about rolling it toward the nest, thus treating it as an egg. It then paused and dug into it with its beak. The meal went on for a minute or more. On going out to change plates in my camera, I put the cake in the empty nest. On its return the bird began to eat it. After a few pecks it settled down to incubate it . . . . . There are two distinguishable facts in the experiment. The first is that the gull perceived a cake as the functional of an egg, as something to be retrieved and incubated. That is no more remarkable than the retrieving and incubation of other egg-equivalents, such as balls, reels and boxes. The second is that, in a few instants, the cake, while remaining unchanged for the observer, twice changed its

meaning for the bird. From being egg-equivalent to be retrieved it became something to eat; and, when put in the nest, it passed from eatable to something to incubate. The change of meaning was not the effect of any change in the cake; it was the effect of some change in the bird itself, a change that turned on the interaction of the two drives involved; hunger and broodiness' (1940, p. 64).

We must now consider in some detail the conditions in which an egg or egg-substitute acquires 'to be retrieved' valence, or loses special valence completely.

In the normal course of events a gull, on leaving the nest, may accidentally roll an egg out; when it returns, it rolls the egg back into the nest, placing its beak on the farther side of the egg and rolling or scooping it back into the nest. Though the normal end or completion of the action is incubation, the retrieving action is a separate one from the act of settling the egg into a position for incubation, and is not entirely dependent upon there being an unsatisfied contact-need. This is shown by the fact that a gull sitting on a full clutch of eggs may yet roll into the nest several more eggs which have been placed nearby. It appears, therefore, that eggs in proximity to the nest may have an imperative 'to be retrieved' valence for the brooding bird; they may, as it were, 'demand' to be retrieved.

To possess this kind of functional valence the egg must be fairly close to the nest; the limiting distance is somewhere about 3 feet from the centre of the nest, or about $2\frac{1}{2}$ feet from its edge. Beyond this distance few, if any, birds will roll the egg back to the nest. It is to be noted that this maximum extension of the zone of valence is dependent upon the nest being empty; if there are eggs in it, about 50 per cent of the birds will fail to roll in from 1 foot from the nest centre. The perceptual situation which leads to retrieving appears, then, to be 'egg-object seen as related functionally to nest', and the relating activity is strengthened if the nest is felt to be empty. Beyond a certain distance the egg-object cannot be related in the bird's mind with the nest, and it loses its 'to be retrieved' valence. There is more involved than a direct visual 'seeing together' of egg and nest, for the egg is generally viewed from the nest itself; the relating of the two must be a 'central' or mental activity. If the egg is too far from the nest for this relation to be established, it loses its functional valence. It may be disregarded altogether; in such case, 'it ceases to have any significance for the bird, is left lying indefinitely, and becomes, as it were, part of the landscape' (p. 146). The bird may walk over or past the egg, paying no attention to it. The image of the egg is, we might say, *passively received* by the bird; as it does not arouse attention, it is not, properly speaking, *perceived*. This is a phenomenon with which our own experience makes us familiar; on a country walk, for instance, especially if we are preoccupied, many things and events that pass before our eyes are not noticed, not perceived, because our attention is not directed towards them. It appears, then, that perception is an active function, dependent upon attention; it is more than a passive reception of sensory impressions.

In the case of the gull, we judge that the isolated egg is not perceived because the gull *does* nothing about it; it has clearly no functional

valence beyond that of any other solid object or surface in the bird's environment. We have no reason to think that the gull perceives any 'thing' as a mere object for contemplation or detached interest, to be noticed or ignored at will. When the gull ignores the egg, this simply means that the egg does not arouse any attention-perception-action response; we can further say that the reason why it does not excite the retrieving response is that the bird fails to perceive it as functionally related to the nest, that is, as something to be moved into the nest, something with 'to be retrieved' valence.

But the isolated egg is not always ignored. It may be incubated *in situ*, and a new nest built round it. In this case, the egg is perceived as 'something to be incubated'; it arouses attention and perception as an 'incubatable' object, or rather an object 'to be incubated', an 'incubandum'.

When the eggs are removed from the nest and placed outside at the critical distance of $1\frac{1}{2}$ feet from the centre, they may be treated in four different ways, according to the reaction of the individual birds. Of 26 birds, one-half rolled an egg or eggs back into the nest, four ignored them completely, one sat on the eggs and built a nest round them (after rolling the eggs to the edge of the original nest), while the rest showed incipient rolling or incubating responses, usually alternating between them. It is noteworthy also that one of the four that ignored the functional possibilities of the eggs treated them as 'something to be guarded' when another gull threatened to attack them, driving away the intruder.

We reach, then, the remarkable conclusion that the same perceptual object may be (1) passively received, i.e., not attended to, or perceived, so far as we may judge from the absence of any response; (2) actively attended to, perceived, and reacted to as 'something to be rolled into the nest'; (3) the same, but reacted to as 'something to be incubated'; (4) the same, but treated as 'something to be guarded'. And the same bird may show two or more of these quite different responses in rapid succession. Which response is given depends to a considerable extent upon the perceptual situation, e.g., distance of egg from nest, presence or absence of an intruder. It seems, then, that what the bird reacts to is the *practical meaning for it* of the perceived object in the given perceptual situation—what it can or must do about it.

The actual sensory characteristics of the object may vary within wide limits without its ceasing to be valent. We have seen that the gull will incubate a whole series of different objects placed in the nest, provided they satisfy more or less adequately the contact-need of the brooding spots. It has also been shown by Kirkman (1937, 1941) that the gull may retrieve and move into the nest a range of substitute objects placed in close proximity to it, such as white or coloured pot eggs, red and blue wooden eggs, balls, cubes, cylinders and a flat circular box; not all the gulls will do this, and some will retrieve only egg-shaped substitutes. There is evidence also that the birds distinguish differences between eggs and substitutes, preferring real eggs to egg-shaped substitutes, and egg-shaped substitutes to objects of other shapes. Later experiments showed that some objects, such as an egg-shaped object of cloth or tissue paper, a small rubber balloon, a cartridge case and an open

pine cone, were completely ignored, though some of these would be incubated, if placed in the nest.

Apparently, then, within certain limits of shape and appearance, any smallish object close to the nest may be treated as functionally equivalent to an egg and be moved into the nest.

The explanation is, I think, this : in its breeding state, the gull has a perception-action disposition to shift back into the nest any egg that falls or has been accidentally pushed out of the nest. It is innately or instinctively predisposed to deal with this normal contingency in an appropriate way. When, by the intervention of the experimenter, objects somewhat similar as regards size and shape appear near the nest, the bird treats the abnormal objects in the same way as the normal, adopts the same way of dealing with them, even though they look different.

On the other hand, when the normal object, the egg, is placed at an abnormal distance from the nest, at a distance to which it would not normally roll, the instinctive perception-action disposition to retrieve it tends to break down ; the bird is predisposed to deal effectively only with a more or less usual or normal situation, and fails to respond effectively or to respond at all when the situation becomes too abnormal. It must be remembered that Kirkman's experiments, simple though they were, presented the birds with problems which neither they nor their ancestors had ever been called upon to solve, and that instinctive behaviour is characteristically adapted to deal only with what is normal for the species.

Incubation of egg-substitutes in the nest (provided they have certain valent characteristics) is to be explained in the same way. Objects in the nest are normally eggs, and the normal response to them is incubation ; this normal treatment is blindly and instinctively applied to objects in the nest that are not eggs. If, however, they do not have the tactual characteristics of eggs, incubation attempts soon cease.

Whether the interpretation offered is the true one or not, one thing seems to be certain, that the gull does not recognize an egg *as such*, as having a continuous existence and remaining the same thing in all circumstances, even though it may distinguish differences between eggs and other objects. According to the psychobiological situation, an egg has for the bird quite different functional valence or ' meaning for action ', or it may have no special functional valence at all. Also other objects, somewhat remotely resembling an egg, in the same situation, may be treated in the same way as eggs. It is, therefore, *valence*, practical or functional meaning, that is important, *not* appearance.

That the gull does not recognize an egg (its own or another gull's) *as such* is, of course, not surprising, for we have no reason to think that it can form any explicit concepts whatever, and ' egg ' in this sense is clearly a concept. Its mental activity takes place on the perceptual level, where action follows directly on perception and requires no explicit or conceptual thought for its initiation or fulfilment. Our own thinking is done on the conceptual plane ; we form ideas and concepts, abstracting from the particular to the general ; we have class-names for objects that resemble one another sufficiently, and these names and concepts may have no reference to our particular needs or possibilities of action. Not so with the bird. We must be very careful to avoid an

anthropomorphic interpretation of its behaviour, one which implies that it has the power of conceptual thought; its behaviour is predominately perceptual and practical.

It is able to discriminate gulls' eggs from other objects, and in certain conditions it treats these (and sometimes other) objects in the same way, as functionally equivalent; *practically*, they are for it the same. If it were able to form a simple concept on this practical or functional basis, and were able to give these objects a common name, it would still have no general word for 'egg', but separate words for 'broodable object', 'retrievable object', and so on.

That is just what happens in human subjects who have suffered certain cortical lesions. In cases of amnesic aphasia the words for general concepts are 'lost', and the words used refer to the particular concrete object which is perceived. 'How very concretely such words are apprehended may be demonstrated by the following example. When, to such a patient as ours, a knife was offered with a pencil, she called the knife a "pencil-sharpener"; when the knife was offered with an apple, it was to her an "apple-parer"; when offered with a potato, it was a "potato peeler"; in company with a piece of bread, it became a "bread knife"; and with a fork it was "knife and fork". The word "knife" alone she never uttered spontaneously, and when she was asked "Could we not always call it simply knife", she replied promptly "No"'. (Goldstein, 1940, p. 78.) Goldstein points out that this curious use of words is a consequence of the fact that patients of this kind have lost 'the capacity to create any sort of abstraction', or to think conceptually. What is also highly significant is the fact that the knife in different situations is characterized *functionally*, i.e., with special reference to its possible immediate use by the patient. This case, it seems to me, gives us a close and illuminating parallel with the behaviour of the gull, and, indeed, of animals generally—behaviour on the perceptual, concrete and practical level, where functional valence, i.e., meaning for action, is far more important than mere sensory appearance, and the power to form abstract concepts and use general class-names is completely absent. In action there may be generalization, inasmuch as classes of objects may be treated in practice as functionally equivalent, but no class-concept is formed, even on this practical basis; generalization remains on the perceptual or practical level, and conceptual thought is absent.

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[Part 2, pp. 69–208, *published 21 January 1944.*]

CONTENTS (*continued*).

Page

Proceedings, 11 March 1943 80

A specimen of the Mexican Loggerhead Turtle (*Caretta kempi*) stranded at Polzeath, Cornwall. By Malcolm A. Smith. [Exhibit.] 81

Synopses of the British Fauna—No. 1. Opiliones. By Theodore H. Savory 81

Field Studies on Valeriana officinalis Linn. in the Cotswold Hills. By T. A. Sprague 93

Proceedings, 25 March 1943 72

Some aspects of Polarity in the distribution of organisms. By R. S. Wimpenny. [Abstract.] 105

The Ecological Society's scheme for a Biological Flora of the British Isles. By A. R. Clapham 107

Proceedings, 8 April 1943 111

The theory of Continental Drift. By Sir Thomas H. Holland. 112

Proceedings, 13 May 1943 125

An abnormal Tulip. By Anthony Belt. [Exhibit.] 125

Aërial tuber-production on the Potato plant. By E. Marion Delf. [Exhibit.] 126

Plasmodium struthionis, sp. n., from Sudanese Ostriches and *Sarcocystis salvelini*, sp. n., from Canadian Speckled Trout (*Salvelinus fontinalis*), together with a record of a *Sarcocystis* in the Eel Pout (*Zoarces angularis*). By Annie Porter. [Abstract.] 127

Some problems associated with Nectar, Pollen and Honey. By John Pryce-Jones 129

Proceedings of the Anniversary Meeting 175

Senecio squalidus and *S. vulgaris* from Norwich. By H. J. Howard. [Exhibit.] 175

The Treasurer's Report and Accounts for the Year ended 30 April 1943 175

The Librarian & Assistant Secretary's Report 181

The President's Review 182

PRESIDENTIAL ADDRESS.—The Stereotypy of Instinctive Behaviour. With an Appendix on Valence as 'Meaning for Action'. By Dr. E. S. Russell, O.B.E. 186